IMPERIAL AGRICULTURAL
RESEARCH INSTITUTE, NEW DELHI.

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY

OF LONDON.

1921, pp. 447–887,

WITH 18 PLATES AND 184 TEXT-FIGURES.

313591
IARI

PRINTED FOR THE SOCIETY,
SOLD AT ITS HOUSE IN REGENT'S PARK.
LONDON:
MESSRS. LONGMANS, GREEN, AND CO.
PATERNOSTER ROW.

LIST
OF THE
COUNCIL AND OFFICERS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.
1921.

Patron.
His Majesty The King.

COUNCIL.
His Grace The Duke of Bedford, K.G., F.R.S., *President.*

Alfred H. Cocks, Esq., M.A.
Charles Drummond, Esq., *Treasurer.*
Alfred Ezra, Esq., O.B.E.
The Right Hon. The Viscount Grey, K.G., P.C.
Sir Sidney F. Harmer, K.B.E., M.A., Sc.D., F.R.S., *Vice-President.*
Prof. James P. Hill, D.Sc., F.R.S., *Vice-President.*
William Huntsman, Esq.
Major The Lord Alastair Robert Innes-Ker.
Prof. Ernest W. MacBride, D.Sc., F.R.S., *Vice-President.*
Col. Sir Henry McMahon, G.C.M.G., K.C.I.E.
E. G. B. Meade-Waldo, Esq., *Vice-President.*
P. Chalmers Mitchell, Esq., C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*
The Earl of Onslow, O.B.E.
Major Albert Pam, O.B.E.
The Lord Queenborough.
His Grace The Duke of Rutland, K.G.
Major Richard S. Taylor.
A. Trevor-Battye, Esq., M.A.
Anthony H. Wingfield, Esq., *Vice-President.*
A. Smith Woodward, Esq., LL.D., F.R.S., *Vice-President.*

PRINCIPAL OFFICERS.
P. Chalmers Mitchell, C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*
R. I. Pocock, F.R.S., F.L.S., *Curator of Mammals and Resident Superintendent of the Gardens.*
D. Seth-Smith, *Curator of Birds and Inspector of Works.*
Edward G. Boulenger, *Curator of Reptiles.*
Miss L. E. Cheesman, F.E.S., *Curator of Insects.*
Dr. C. F. Sonntag, Ch.B., *Anatomist.*
Dr. N. S. Lucas, M.B., Ch.B., *Pathologist.*
R. J. Ortlepp, M.A., *Hon. Parasitologist.*
F. Martin Duncan, F.R.M.S., *Librarian.*
F. W. Bond, *Accountant.*
W. H. Cole, *Chief Clerk.*

LIST OF CONTENTS.

1921, pp. 447–887.

EXHIBITIONS AND NOTICES.

Page

Sir S. F. HARMER, K.B.E., F.R.S. Exhibition of, and remarks upon, a mounted specimen of a young female *Rhinoceros sondaicus* 643

Mr. THOS. GERRARD, F.Z.S. Exhibition of, and remarks upon, photographs of the skeleton of an old male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie) 643

Lord ROTHSCHILD, F.R.S., F.Z.S. Exhibition of, and remarks upon, a mounted specimen of a male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie) 643

Mr. D. SETH-SMITH, F.Z.S. Exhibition of, and remarks upon, a series of skins and photographs of polyandrous Birds 644

Dr. CHAS. F. SONNTAG, F.Z.S. Exhibition of, and remarks upon, some abnormalities in the Carnivora 644

Mr. L. T. HOGBEN, F.Z.S., and Mr. E. A. SPAUL. Exhibition of, and remarks upon, effect of Pineal Gland administration on Frog Tadpoles 644

The SECRETARY. Report on the Additions to the Society's Menagerie during the month of April, 1921........... 644

Miss L. E. CHEESMAN, F.E.S. Exhibition of, and remarks upon, lantern-slides of the larval stages of some Hydropsychidæ 644

Major STANLEY S. FLOWER, O.B.E., F.Z.S. Exhibition of, and remarks upon, examples of three species of Egyptian Jerboas 645

Page

Major Stanley S. Flower, O.B.E., F.Z.S. Exhibition of, and remarks upon, living specimens of *Testudo leithii* and *T. ibera* 645

Dr. P. Chalmers Mitchell, C.B.E., F.R.S., F.Z.S. Exhibition of, and remarks upon, photographs of the Death-mask of a young Gorilla 645

Dr. F. M. Chapman. An account of the distribution of Bird-life in the Urubamba Valley of Peru 645

Prof. J. P. Hill, F.R.S., V.P.Z.S. Exhibition of, and remarks upon, a series of lantern-slides of Marsupial embryos 646

The Secretary. Report on Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1921 883

Mr. M. A. C. Hinton. Exhibition of an embryo African Elephant 885

Mr. G. E. Boulenger, F.Z.S. Exhibition of photographs of a Common Grass Snake swallowing a Viper 886

Mr. F. Martin Duncan, F.Z.S. Exhibition of cinematograph films of Marine Animals 886

Mr. D. Seth-Smith, F.Z.S. Exhibition of photographs of the Sacred Ibis nesting in the Society's Gardens 886

Prof. G. Elliot Smith, F.R.S., F.Z.S. An account of the habits of *Tarsius*, illustrated by lantern-slides 886

Mr. Edgar P. Chance, M.A., M.B.O.U. Exhibition of cinematograph films illustrating the laying-habits of the Cuckoo (*Cuculus canorus*) and the life of the Young Cuckoo 886

The Secretary. Report on the Additions to the Society's Menagerie during the month of October, 1921 886

Mr. A. S. Le Souëf, C.M.Z.S. Exhibition of photographs illustrating the early life-history of *Ornithorhynchus*. 887

Dr. A. Smith Woodward, F.R.S., V.P.Z.S. Exhibition of a Human Skull and other remains from Broken Hill, North Rhodesia 887

PAPERS.

Page

23. The Geographical Distribution of Orthopterous Insects in the Caucasus and in Western Asia. By B. P. Uvarov. (Map.) 447

24. The Auditory Bulla and other Cranial Characters in the Mustelidæ. By R. I. Pocock, F.R.S., F.Z.S. (Text-figures 14–18.) 473

25. On the Venous System of the Lizard *Varanus bengalensis* (Daud.). By Gobind Singh Thapar, M.Sc. (Text-figures 1–4.) 487

26. Abnormalities in the Common Frog (*Rana temporaria*). By J. H. Lloyd, M.Sc., F.Z.S. (Text-figure 1.) 493

27. Comparative Anatomy of the Tongues of the Mammalia.—IV. Families 3 and 4. Cebidæ and Hapalidæ. By C. F. Sonntag, M.D., F.Z.S., Anatomist to the Society. (Text figures 37–52.) 497

28. Note on the Skull of *Dinotherium giganteum* in the British Museum. By C. W. Andrews, D.Sc., F.R.S., F.Z.S. (Text-figures 1–4.) 525

29. On the External Characters of some Species of Lutrinæ (Otters). By R. I. Pocock, F.R.S., F.Z.S. (Text-figures 19–21.) 535

30. The Comparative Anatomy of the Koala (*Phascolarctos cinereus*) and Vulpine Phalanger (*Trichosurus vulpecula*). By Chas. F. Sonntag, M.D., F.Z.S. (Plates V., VI.; Text-figures 53–63.) 547

31. New Indian Drilid Beetles. By S. Maulik, F.Z.S. (Text-figures 1–5.) 579

Page

32. On some Abnormalities in the Carnivora. By CHARLES F. SONNTAG, M.D., F.Z.S. (Text-figures 64–65.)...... 587

33. The External Characters of the Koala (*Phascolarctos*). By R. I. POCOCK, F.R.S., F.Z.S. (Text-figures 22–26.) 591

34. The Nestling Feathers of the Mallard, with Observations on the Composition, Origin, and History of Feathers. By J. COSSAR EWART, M.D., F.R.S., F.Z.S. (Plates I.–X.; Text-figures 1–14.)...................... 609

35. On some new Genera and Species of Anomodont Reptiles from the Karroo Beds of South Africa. By R. BROOM, F.R.S., C.M.Z.S. (Text-figures 28–45.) 647

36. The Cichlid Fishes of Lake Nyassa. By C. TATE REGAN, M.A., F.R.S., F.Z.S., Keeper of Zoology, British Museum (Natural History). (Plates I.–VI.; Text-figures 1–30.)... 675

37. Note on the Systematic Position and Distribution of the Actinian *Sagartia luciæ*. By J. PLAYFAIR McMURRICH, C.M.Z.S. (Text-figures 1–4.)........... 729

38. The Comparative Anatomy of the Tongues of the Mammalia.—V. Lemuroidea and Tarsioidea. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society. (Text-figures 66–69.) 741

39. The Comparative Anatomy of the Tongues of the Mammalia.—VI. Summary and Classification of the Tongues of the Primates. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society................. 757

40. On some new Parasitic Mites. By STANLEY HIRST, F.Z.S. (Text-figures 16–43.)........................... 769

41. On the External Characters and Classification of the Mustelidæ. By R. I. POCOCK, F.R.S., F.Z.S. (Text-figures 27–39.)... 803

42. *Megalohyrax* Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt. By H. MATSUMOTO. (Text-figures 1–6.)... 839

Page

43. Contributions to the Visceral Anatomy and Myology of the Marsupialia. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society. (Text-figures 70–79.) 851

Alphabetical List of Contributors........ viii

Index of Illustrations xiii

Index xvii

ALPHABETICAL LIST

OF THE

CONTRIBUTORS,

With References to the several Articles contributed by each.

(1921, pp. 447–887.)

Page

ANDREWS, C. W., D.Sc., F.R.S., F.Z.S.

Note on the Skull of *Dinotherium giganteum* in the British Museum. (Text-figures 1–4.) 525

BOULENGER, E. G., F.Z.S.

Exhibition of photographs of a Common Grass Snake swallowing a Viper 886

BROOM, R., F.R.S., C.M.Z.S.

On some new Genera and Species of Anomodont Reptiles from the Karroo Beds of South Africa. (Text-figures 28–45.) 647

CHANCE, EDGAR P., M.A., M.B.O.U.

Exhibition of Cinematograph Films illustrating the laying-habits of the Cuckoo (*Cuculus canorus*) and the life of the young Cuckoo 886

CHAPMAN, Dr. FRANK M.

An Account of the Distribution of Bird-life in the Urubamba Valley of Peru 645

Page

Cheeseman, Miss L. E., F.E.S.

Exhibition of, and remarks upon, lantern-slides of the larval stages of some Hydropsychidæ 644

Duncan, F. Martin, F.Z.S. (Librarian to the Society).

Exhibition of Cinematograph Films of Marine Animals 886

Ewart, J. Cossar, M.D., F.R.S., F.Z.S.

The Nestling Feathers of the Mallard, with Observations on the Composition, Origin, and History of Feathers. (Plates I.–X.; Text-figures 1–14.) 609

Flower, Major Stanley S., O.B.E., F.Z.S.

Exhibition of, and remarks upon, examples of three species of Egyptian Jerboas 645

Exhibition of, and remarks upon, living specimens of *Testudo leithii* and *T. ibera* 645

Gerrard, Thos., F.Z.S.

Exhibition of, and remarks upon, photographs of the skeleton of an old male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie) 643

Harmer, Sir Sidney F., K.B.E., M.A., F.R.S., V.P.Z.S.

Exhibition of, and remarks upon, a mounted specimen of a young female *Rhinoceros sondaicus* 643

Hill, Prof. J. P., F.R.S., V.P.Z.S.

Exhibition of, and remarks upon, a series of lantern-slides of Marsupial embryos 646

Hinton, M. A. C.

Exhibition of an embryo African Elephant 885

Hirst, Stanley, F.Z.S.

On some new Parasitic Mites. (Text-figures 16–43.) . 769

Page

HOGBEN, L. T., F.Z.S., and SPAUL, E. A.

Exhibition of, and remarks upon, effect of Pineal Gland administration on Frog Tadpoles 644

LE SOUËF, A. S., C.M.Z.S.

Exhibition of photographs illustrating the early Life-history of *Ornithorhynchus* 887

LLOYD, J. H., M.Sc., F.Z.S.

Abnormalities in the Common Frog. (Text-figure 1.) 493

MATSUMOTO, H.

Megalohyrax Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt. (Text-figures 1–6.) 803

MAULIK, S., F.Z.S.

New Indian Drilid Beetles. (Text-figures 1–5.) 579

McMURRICH, J. PLAYFAIR, C.M.Z.S.

Note on the Systematic Position and Distribution of the Actinian *Sagartia luciæ*. (Text-figures 1–4.) 729

MITCHELL, Dr. P. CHALMERS, C.B.E., F.R.S. (Secretary to the Society).

Report on the Additions to the Society's Menagerie during the month of April, 1921 644

Exhibition of, and remarks upon, photographs of the Death mask of a young Gorilla 645

Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1921 883

Report on the Additions to the Society's Menagerie during the month of October, 1921 886

Page

Pocock, R. I., F.R.S., F.Z.S. (Curator of Mammals).

The Auditory Bulla and other Cranial Characters in the Mustelidæ. (Text-figures 14–18.) 473

On the External Characters of some Species of Lutrinæ (Otters). (Text-figures 19–21.) 535

The External Characters of the Koala (*Phascolarctos*). (Text-figures 22–26.) 591

On the External Characters and Classification of the Mustelidæ. (Text-figures 27–39.) 803

Regan, C. Tate, M.A., F.R.S., F.Z.S., Keeper of Zoology, British Museum (Natural History).

The Cichlid Fishes of Lake Nyassa. (Plates I.–VI.; Text-figures 1–30.) 675

Rothschild, Lionel Walter, Lord, D.Sc., F.R.S., Ph.D., F.Z.S.

Exhibition of, and remarks upon, a mounted specimen of a male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie) 643

Smith, D. Seth-, F.Z.S. (Curator of Birds).

Exhibition of, and remarks upon, a series of skins and photographs of polyandrous Birds 644

Exhibition of photographs of the Sacred Ibis nesting in the Society's Gardens 886

Smith, Prof. G. Elliot, F.R.S., F.Z.S.

An Account of the habits of *Tarsius*, illustrated by lantern-slides 886

Sonntag, Charles F., M.D., F.Z.S. (Anatomist to the Society).

Comparative Anatomy of the Tongues of the Mammalia.—IV. Families 3 and 4. Cebidæ and Hapalidæ. (Text-figures 37–52.) 497

Page

Sonntag, Charles F., M.D., F.Z.S. (*continued*).

The Comparative Anatomy of the Koala (*Phascolarctos cinereus*) and Vulpine Phalanger (*Trichosurus vulpecula*). (Plates V., VI.; Text-figures 53-63.) 547

On some Abnormalities in the Carnivora. (Text-figures 64, 65.) 587

Exhibition of, and Remarks upon, some Abnormalities in the Carnivora 644

The Comparative Anatomy of the Tongues of the Mammalia.—V. Lemuroidea and Tarsoidea. (Text-figures 66-69.) 741

The Comparative Anatomy of the Tongues of the Mammalia.—VI. Summary and Classification of the Tongues of the Primates 757

Contributions to the Visceral Anatomy and Myology of the Marsupialia. (Text-figures 70-79.) 851

Thapar, Gobind Singh, M.Sc.

On the Venous System of the Lizard *Varanus bengalensis* (Daud.). (Text-figures 1-4.) 487

Uvarov, B. P.

The Geographical Distribution of Orthopterous Insects in the Caucasus and in Western Asia. (Map.) 447

Woodward, Dr. A. Smith, F.R.S., V.P.Z.S.

Exhibition of a Human Skull and other remains from Broken Hill, North Rhodesia 887

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

23. The Geographical Distribution of Orthopterous Insects in the Caucasus and in Western Asia. By B. P. Uvarov *.

(With Map.)

[Received October 25, 1920; Read March 8, 1921.]

Introduction.

In 1913 I undertook the systematic study of the Orthopteran fauna of the Caucasus and neighbouring countries (Asia Minor, Armenia, Northern Persia), based on the large collections of the Caucasian Museum in Tiflis and literary sources, as well as upon my own investigations in Northern Caucasus (in 1911–1914) and in Transcaucasia (in 1915–1919). This work offered great difficulties, as our knowledge concerning the systematic and geographical distribution of the Orthoptera, and those of Western Asia in particular, is as yet very incomplete. Besides, the war deprived me of the possibility of referring to Western European scientific centres and of obtaining from them the necessary literature and information. The materials which I have had before me, though not very extensive, give different impressions concerning the faunas of different districts, and some of the latter are still awaiting more careful investigation. I think, however, that it would be of some use for these future investigations if I gave a short summary of the chief zoogeographical results I have gained from my studies, incomplete and insufficient though they may be. I hope these results will be of interest to every zoogeographist studying the distribution of animals in the southern parts of the Palæarctic region.

---

* Communicated by S. A. Neave, F.Z.S.

Before investigating more minutely the distribution of Orthoptera in the territory under consideration, it is necessary to give some information concerning the zoogeographical division of the Palæarctic region based on my studies of this group, for this division differs in some respects from those of other authors founded on the distribution of other animal groups.

The subregions into which the Palæarctic region may be divided are four in number: Boreal, Steppe, Mediterranean, and Eremian. The chief characteristics of these are as follows:—

The Boreal subregion includes the whole zone of the forests of Northern Europe and Asia, but some representatives of its characteristic Orthopteran fauna penetrate farther on northwards—into the zone of the Arctic tundras which has not its own Orthopteran fauna. The Orthopteran fauna of the Boreal subregion is very poor, both in species and in specimens; the suborders Mantodea and Phasmodea are entirely absent from it, and of the Gryllodea we only find the *Gryllus domesticus* here. As leading characteristics of Boreal fauna should be regarded: *Chrysochraon dispar*, *Stenobothrus viridulus*, *Gomphocerus sibiricus*, *Mecostethus grossus*, *Psophus stridulus*, and *Podisma pedestris* from Acridiodea, and *Leptophyes punctatissima*, *Meconema thalassinum*, and *Olynthoscelis griseoaptera* from Locustodea.

The great distance between our country and the Boreal subregion causes the Boreal fauna to be of very little importance in the composition of our fauna. Nevertheless, in some districts of the Caucasus, as we shall see later on, the influence of the Boreal fauna is rather striking: in some mountainous districts we may find the typical boreal species, which are, at the same time, absent from the intermediate areas between the Caucasus and the Boreal subregion. These species with such discontinuous range of distribution are of great importance to the history of the fauna of the Caucasian mountains, as they give us a hint concerning the former contact of this fauna with that of the Boreal subregion; later on this contact was interrupted, but the cause of this interruption is still unknown to us with certainty; we can only suppose that this immediate connection between the Orthopteran faunas of the Caucasus and of the Boreal subregion took place during the Glacial period, and ceased after this period had given place to a warmer and drier one, when the Boreal elements of the fauna retreated to the North, leaving a few relics in the high mountainous districts of the Caucasus.

The Orthopteran fauna of the Steppe subregion is rather rich and includes many typical forms. The most important character of this fauna is the presence of a large number of species of the genus *Stenobothrus*. The Steppe fauna in Europe shows distinctly marked affinities with the Siberian, and we should suppose that its representatives have migrated into Europe from Asia.

The Steppe fauna penetrates into our country through the steppes of North-western Caucasus, which belong to the Steppe subregion, and through Daghestan some of its elements reach Transcaucasia, as well as the mountainous districts of Caucasus Minor, Armenia, Kurdistan, and Anatolia as far as the northern limits of the Eremian subregion. On the other hand, the Steppe fauna also penetrates into Anatolia through the Balkan Peninsula. It is evident that the influence of this fauna on the fauna of our country must be very great, and so it is, as we shall see later on.

The Mediterranean subregion comprises the north-western mountainous extremity of Africa (Morocco, Algeria, and Tunis—but the mountains only and not the plains, which belong to the Eremian subregion), Spain, the southern coast of France, Italy, the shores of the Adriatic Sea, the Balkan Peninsula south of the Balkan Mountains, the islands of the Mediterranean Sea, and Anatolia. The Mediterranean fauna of Orthoptera is extremely rich, including about 16 Mantodea, 7 Phasmodea, 162 Acridiodea, 317 Locustodea, and 62 Gryllodea. Besides its richness this fauna is remarkable for a large number of peculiar species: out of 564 species which are known of it, 424 or 75 per cent. are endemic. Some large families of Locustodea have their centre of development and distribution here, for example Sagidæ, Decticidæ, Bradyporidæ, and, partly, Phaneropteridæ.

The more detailed study of the Mediterranean fauna allows us to conclude that it may be divided into two very distinct groups of species: Western and Eastern. The first has its centre in Spain and North-western Africa, from where its representatives disperse to the East and North-east; while the second flourishes in the southern part of the Balkan Peninsula and in adjacent parts of Anatolia, sending its migrants into north-western, northern, north-eastern (into the Steppe subregion), and eastern directions. According to this distinction of the faunas we may divide the Mediterranean subregion into two zoogeographical provinces—Western or Tyrrhenian and Eastern or Balkano-Anatolian. The Tyrrhenian fauna is of no importance to us, as it cannot influence the composition of the fauna of the Caucasus, but of much greater value is the Balkano-Anatolian fauna. This fauna is very rich and has many characteristic points: here we find exceedingly rich development of endemic Sagidæ, of apterous Phaneropteridæ (*Isophya*, *Pœcilimon*), of the genera *Platycleis*, *Olynthoscelis*, *Drymadusa*, *Dolichopoda*; some species of *Stenobothrus* and the genera *Nocarodes* (with six species) and *Callimenus* (with two species) are peculiar to it.

The Balkano-Anatolian fauna occupies the greatest part of the country which we are now studying. Through Asia Minor, which belongs entirely to this zoogeographical province, through Armenia, and along the southern and eastern shores of the Black Sea, the Balkano-Anatolian fauna penetrates into the forest districts of Transcaucasia, giving place to the Eremian fauna in the desert plains of Eastern Transcaucasia and in the dry rocky districts of Persia; we meet it again on the southern shore of the Caspian Sea—in the district of Talysh, which is remarkable for its wet subtropical climate. Some typical Balkano-Anatolian faunistic elements also reach the Caucasus from the north, wandering from their native home along the western and northern shores of the Black Sea through the adjacent steppes of South Russia.

To the south of the Mediterranean subregion lies the vast Eremian subregion, which includes all the deserts of North Africa (Sahara, Libyan desert, Egypt), Sinai peninsula, Northern Arabia, Mesopotamia, Persia, the whole of the Aralo-Caspian impression; perhaps, also, the great deserts of Chinese Turkestan and Mongolia, the Orthopteran fauna of which is but little investigated as yet, belong to it. The Orthopteran fauna of the Eremian subregion has many peculiarities if compared with the Mediterranean, and I cannot agree with most of the zoogeographists* who usually unite them together. In support of my opinion I give the following table:—

	Mantodea.	Phasmodea.	Acridiodea.	Locustodea.	Gryllodea.	Total.
Mediterranean fauna.						
Total number of species..................	16	7	162	317	62	564
Number of species which do not penetrate into the Eremian subregion...	9	7	130	299	51	496
Endemics..................................	9	7	108	259	41	424
Percentage of endemism...................	56 %	100 %	67 %	82 %	66 %	75 %
Common with the Eremian subregion.	7	0	32	18	12	69
Eremian fauna.						
Total number of species..................	53	9	137	45	31	275
Number of species which do not penetrate into the Mediterranean subregion	46	9	105	27	19	206
Endemics..................................	42	9	99	24	16	190
Percentage of endemism	79 %	100 %	72 %	53 %	51 %	70 %

It is evident from this table that the affinity between the Eremian and the Mediterranean faunas is restricted to 69 species only. Out of these we must, however, not take into consideration 48 very widely distributed species (such as *Paratettix meridionalis*, *Acrotylus insubricus*, *Conocephalus nitidulus*, etc.) and 10 species with great power of flying, which may have wandered from one subregion to another in recent times; there are, therefore, only 11 species common to the Eremian and Mediterranean faunas, *i. e.* but 4 per cent. of the second and less than 2 per cent. of the first of these. These eleven species are as follows: *Fischeria bætica*, *Ameles abjecta*, *Stauronotus hauensteini*, *Œdipoda schochi*, *Nocarodes serricollis*, *Callimenus dilatatus*, *Paradrymadusa sordida*, *Olynthocelis punctifrons*, *Isophya triangularis*, *Gryllus* (*Gryllodes*) *kerkennensis*, and *Gr. lateralis*. Only two of them (both species of *Gryllus*) may be considered as having originated in the Eremian subregion, and they are both to be found in the Mediterranean subregion (in Spain, in Transcaucasia) in proximity to its southern boundaries and on spots with clearly defined desert soil and vegetation; we have the right to believe them to be comparatively recent invaders from the deserts of the Eremian subregion. The remaining nine species are of Balkano-Anatolian origin and do not penetrate deeply into the Eremian subregion, being restricted to its northern mountainous parts with mixed fauna. The relationship of the Mediterranean and of the Eremian faunas is, consequently, practically absent. On the contrary, the same table shows us that the difference between them is a very striking one; 496 species (out of the whole number 564) of Mediterranean Orthoptera do not reach the Eremian subregion, and 206 Eremian species (out of 275) do not go through the northern boundary of this subregion into the Mediterranean. This difference is not numerical only; the family Orthoderidæ is peculiar to the Eremian subregion*, where there are 35 species belonging to it; the family Pamphagidæ is represented in the Mediterranean subregion by 52 species, of which only five penetrate into the neighbouring parts of the Eremian subregion; the family Phaneropteridæ has more than 80 Mediterranean representatives, and only three of them are to be found among the Eremian fauna; two families of Locustodea—Ephippigeridæ (85 species) and Meconematidæ (4 species)—and three of Gryllodea—Gryllomorphidæ (7 species), Myrmecophilidæ (4 species), and Mogisoplistidæ (6 species), which are very important in characterising the Mediterranean fauna, do not extend into the Eremian subregion at all. The generic and specific differences between these two faunas are yet more considerable, but I shall not go into details here, as I suppose the above mentioned facts are sufficient to support my statement that the Eremian subregion is of the same zoogeographical value as the Mediterranean †.

---

* W. L. Sclater was the first who recognised the difference between the Eremian and his "Europasian" (Boreal + Steppe + Mediterranean) subregions, but he included in it the whole of Northern Africa, the western part of which (Morocco, Algeria, and Tunis) must be united with the Mediterranean subregion.

There are only two provinces of the large Eremian subregion which are particularly interesting to us: the Iranian and the

---

* With but one exception—*Geomantis larvoides*—which is Mediterranean endemic.

† I even suppose that, when studying the distribution of Orthoptera, we are right in considering the Eremian subregion of the same value as the whole Palæarctic region: this problem is, however, too great a one to be discussed here, and I hope to return to it at some other time; I am supported in my supposition by the statements of Mr. A. Birula, who, after his studies of the distribution of scorpions, made an Africano-Asiatic region nearly with the same limits as my Eremian subregion (see A. A. Bialynicki-Birula, Arachnoidea Arthrogastra Caucasica, Pars I. Scorpiones.—Mémoires du Musée du Caucase, sér. A, N. 5, 1917).

Turanian. The first of these has some peculiarities in its fauna which are of the greatest interest and value: there are among the rather numerous endemics of the Iranian fauna some very ancient forms (*Paradrymadusa bocquilloni*, *P. persa*, *P. pastuchovi*, *Tropidauchen*, *Platycleis persica*, *Olynthoscelis satunini*, etc.), which belong to the groups characteristic of the Balkano-Anatolian province of the Mediterranean subregion. The presence of these species in the Iranian fauna allows us to conclude that this fauna was in some ancient time in close connection with the Balkano-Anatolian fauna, but afterwards (from the beginning of the dry climatic period in Iranian table-lands) this connection was interrupted, and the further development of the Balkano-Anatolian and of the Iranian fauna went in different directions: the remnants of the "Ancient Mediterranean" fauna in Iran partially died out, partially adapted themselves to the new conditions of life (the "desert" coloration of *Paradrymadusa bocquilloni* and *P. persa*, etc.); and the recent faunas of the Iranian and the Balkano-Anatolian provinces, being of the same origin, are entirely different and belong to the different subregions.

The Iranian fauna occupies a rather large part of Transcaucasia reaching along the western shore of the Caspian Sea as far as the neighbourhood of Petrovsk, as we shall see later on.

The Turanian province of the Eremian subregion comprises Transcaspia and the southern steppes of Kirghizes and Kalmyks along the northern and north-western shores of the Caspian Sea; its Orthopteran fauna is a rather recent derivate of the Iranian which has migrated in northern and north-western directions, invading the parts of land from which the Caspian Sea has recently withdrawn. West of the Caspian Sea (in the Ciscaucasia) the Turanian fauna spreads southwards, coming in contact with direct Iranian migrants somewhere near Petrovsk.

To the south of the Eremian subregion lies the Indo-Ethiopian region, the fauna of which is of some importance for the composition of the fauna of the country we are studying now, where we may find a rather large number of species of undoubtedly Indo-Ethiopian origin, for example: genera *Gelastorrhinus*, *Hierodula*, *Duronia*, *Pyrgomorpha*, *Sphodromerus*, and species—*Tropidopola cylindrica*, *Liogryllus bimaculatus*, etc. All these Indo-Ethiopian elements came into the country under consideration through the Eremian subregion, of which fauna they are very characteristic.

The Zoogeographical Divisions of the Caucasus and neighbouring countries.

Before continuing the study of zoogeographical districts into which the country in question may be divided, I ought to point out that all my conclusions are based exclusively on the study of the geographical distribution of Orthoptera, though I have also taken into consideration the conclusions drawn by the late K. A. Satunin from his study of Caucasian mammals; by Nikolsky—

reptiles and amphibians; Birula (*l. c.*)—scorpions; as well as by other zoologists.

A full list of the Orthoptera, which are known to me from the Caucasus and the neighbouring countries, will be given by me elsewhere.

1. *South Russian Steppe district* (R.M.)*.

The Orthopteran fauna of the open grassy steppes lying to the east of Azov Sea has not yet been sufficiently investigated, and we know but 69 species (3 M† + 32 A + 27 L + 7 G) from it. Notwithstanding, it is evident that this fauna cannot be separated from that of the steppes north of the said sea and of the Black Sea—the steppes of Southern Russia, and it has nothing to do with the fauna of the Caucasus proper. In fact, there is only one species in this fauna which is unknown from the South Russian steppes; it is *Pezotettix giornai*, a Mediterranean species which I think has quite recently penetrated here from the neighbouring Novorossiisk district, and is only restricted to the south-western part of the Azov steppes. We are right, therefore, in regarding the latter as simply being the southern part of the vast South Russian Steppe district. The boundaries of this district, as far as they are lying within the limits of country we are interested in, are not quite defined yet; the southern boundary of it coincides with the northern limit of the forests growing on northern slopes of the Caucasus; its eastern limit is not so sharply marked and is dependent on the westward progression of the Aralo-Caspian (Turanian) flora and fauna along the Valley of Manytsh (see below).

2. *The Kuban-Terek district* (K.-T.).

As I have had the opportunity of studying this district for a rather long time (1911–1914, *i. e.* four years), its fauna is well known to me‡. The number of species known from this district is 77 (2 M + 33 A + 33 L + 9 G) and may be regarded as being very nearly exact. The bulk of this fauna—68 species—is common to it and to the foregoing district, which leads us to the conclusion that the Kuban-Terek district ought to be regarded as belonging to the Steppe subregion. The distinction between the South-Russian fauna and the fauna of this district is based on 13 species. Out of these seven are of well-defined boreal origin: *Stenobothrus nigromaculatus*, *St. ventralis*, *St. scalaris*, *Gomphocerus variegatus*, *Psophus stridulus*, *Leptophyes punctatissima*, and *Olynthoscelis griseoaptera*; they form, no doubt, a rearguard of the relic group of boreal species which retreated from South-Russian steppes,

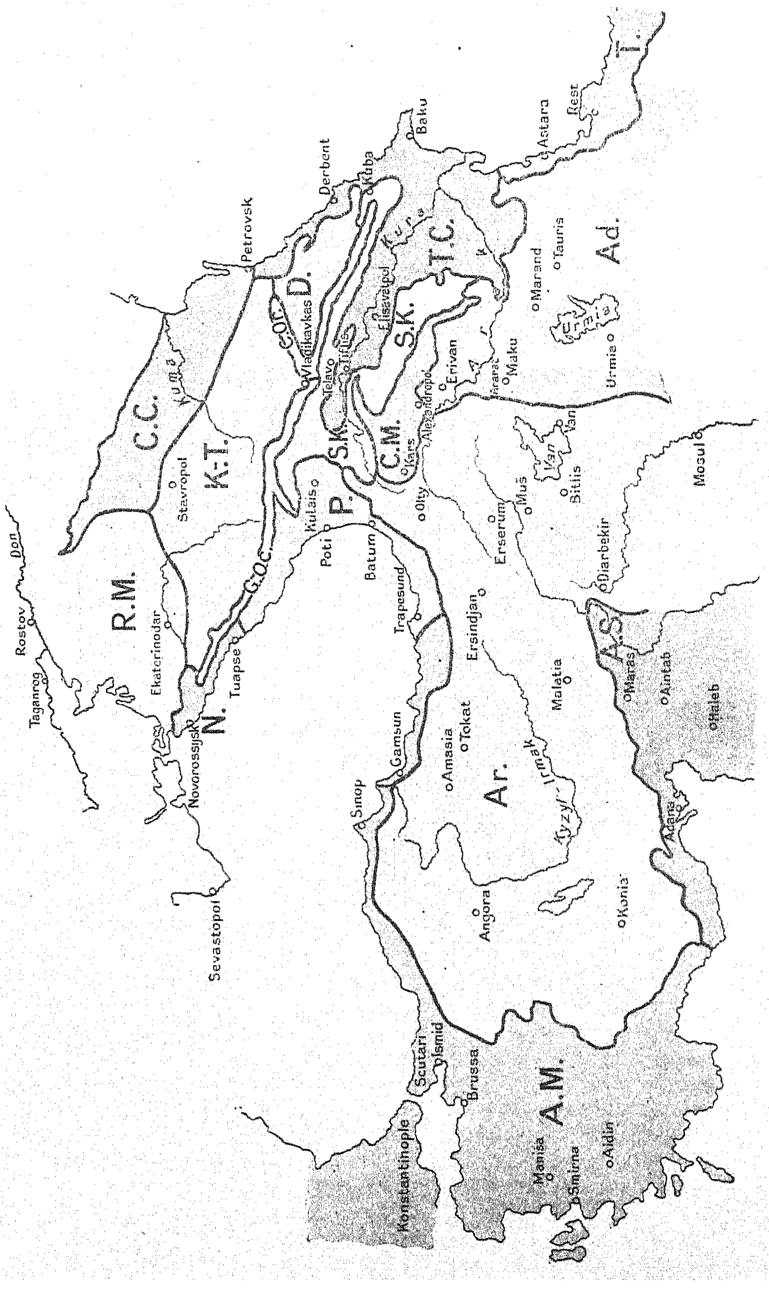
---

* The letters after the name of each district are the initials of their latin names as adopted in my zoogeographical map.

† M=Mantodea, P=Phasmodea, A=Acridiodea, L=Locustodea, G=Gryllodea.

‡ See my publication concerning the Orthopteran fauna of the province Stavropol (Bull. du Musée du Caucase, 1915).

Text-figure 1.



Zoogeographical map of the Caucasus and Western Asia. (For explanation, see p. 472.)

after the end of the Ice age, southwards into the mountains of the Caucasus (see p. 448). Of the remaining six species, four are of Mediterranean (resp. Balkano-Anatolian) origin; these are: *Pœcilimon similis*, *Paradrymadusa beckeri* (peculiar to the Kuban-Terek district, but belonging to a Balkano-Anatolian genus), *Platycleis fusca*, and *Myrmecophila ochracea*, which are to be regarded as immigrants from Transcaucasia. The ways of this migration, doubtless, do not lead across the chain of the Great Caucasus, but I think they go on the west along the shores of the Black Sea, and on the east through the Somkheto-Kakhetian and Daghestan districts (see below). The remaining two species are: firstly, *Gampsocleis schelkovnikovæ*, which has just been described and the zoogeographical physiognomy of which is as yet uncertain; secondly, *Nemobius tartarus*, which has recently penetrated into the Kuban-Terek district from the neighbouring deserts of the Caspian Ciscaucasia.

Thus the Orthopteran fauna of the Kuban-Terek district may be characterised as derived from the South-Russian Steppe fauna, with well-marked indications of southern influences—from Caucasus (forms of boreal origin) and from Anatolia (Balkano-Anatolian species).

The Kuban-Terek district comprises all the northern slopes of the Caucasian mountains, including the adjacent hilly country with insular forests; its northern boundary coincides with the northern limit of these forests on the west and of the grass steppe on the east; while the southern is formed by the upper limit of the forests on the main chain of the Caucasus.

3. *The Daghestan district* (D.).

The fauna of this interesting district has as yet been very little investigated: the whole number of species known from it is only 43 (2 M + 23 A + 12 L + 6 G), which is, certainly, not more than one third of the real number. Notwithstanding, a careful analysis of this fauna allows us to draw some very interesting conclusions as to its composition and origin.

The Daghestanian Orthopteran fauna is in direct contact with the faunas of four districts: Kuban-Terek, Somkheto-Kakhetian, Caspian Transcaucasia, and the Eastern Caucasus. But we find the closest resemblances between our fauna in the two first named districts, and as they belong to distinct subregions (Steppe and Mediterranean respectively), it is an interesting problem to be solved—in which of them the Daghestan should be included.

Out of 39 Daghestanian Orthoptera 34 are common to Daghestan and to the Kuban-Terek district, and only five are distinct, as follows: *Nocarodes serricollis*, *Orphania scutata zacharovi*, *Locusta caudata caudata*, *Decticus verrucivorus verrucivorus*, and *Platycleis daghestanica*. The last named species is peculiar to the Daghestan and of no interest to us; *Nocarodes serricollis* is not to be considered as being characteristic of

Daghestan, since it is not distributed all over this district but confined to its eastern parts; finally, *Locusta caudata caudata*, *Decticus verrucivorus verrucivorus*, and *Orphania scutata zacharovi* are the typical mountain forms and, doubtless, came to Daghestan from the adjacent mountainous district of Eastern Caucasus. It is evident, therefore, that there exists but very little difference between the Daghestanian fauna and that of the Kuban-Terek district, and that this difference is of a recent date and of an accidental origin. On the contrary, the resemblances between them are far deeper, for nearly all the chief characteristic steppe forms (such as *Arcyptera flavicosta flavicosta*, *Celes variabilis variabilis*, *Stauronotus brevicollis*) range into Daghestan, but not farther southwards where (in the Somkheto-Kakhetian district) they are either entirely absent or replaced by other subspecies. Thus, the steppe *Arcyptera flavicosta flavicosta* gives place in the Somkheto-Kakhetian district to the distinct race *A. flavicosta transcaucasica*; *Celes variabilis variabilis* is represented there by the subspecies *C. variabilis carbonaria* and so on. But the most striking difference of the Daghestanian fauna from the Somkheto-Kakhetian (resp. Balkano-Anatolian and even Mediterranean) is in the negative features of the first: the numerous non-flying Phaneropteridæ, which are very characteristic of the Somkheto-Kakhetian fauna, are strange to the Daghestan, where only three of them exist: one *Orphania*, one *Pœcilimon*, and *Leptophyes albovittata* — all three not characteristic of the Somkheto-Kakhetian district; the numerous endemics of the latter do not range into Daghestan at all.

All the above-mentioned facts lead us to the conclusion that the recent Orthopteran fauna of the Daghestan is in more intimate relation to the fauna of the Kuban-Terek district than to that of the Somkheto-Kakhetian. I think, therefore, it should be right to regard Daghestan as an independent zoogeographical district of the Steppe subregion, characterised by the purely steppe Orthopteran fauna with but slight admixture of mountainous forms and of endemics as well as of some "ancient-Mediterranean" species (see p. 452), like *Nocarodes serricollis*, or an undescribed species of *Paradrymadusa*, known to me from Daghestan only in females. I think that further investigations of this interesting district may clear up some details concerning the composition and origin of its fauna but will not change the views expressed above.

Turning to the establishment of the boundaries of this district, we can only definitely state the north-western and south-western ones, which coincide with the lower limits of the alpine district of the Eastern Caucasus. As for the eastern boundary of the Daghestan it should be presumed to go along the extreme eastern chains nearly parallel to the Caspian Sea shore, leaving a narrow strip along the shore itself bearing quite a different Iranian fauna of the district of Caspian Transcaucasia. The most obscure are the boundaries between Daghestan and the districts of Kuban-Terek and of Somkheto-Kakhetia.

4. *The Western Anatolian district* (A.M.).

There are known to us from this district, little investigated though it is, as many as 103 forms of Orthoptera (7 M + 37 A + 48 L + 11 G), which gives evidence that its fauna is a very rich one. As for the composition of this fauna, it may be regarded as the purest expression of the Balkano-Anatolian fauna, which has here its original home.

The most characteristic families of Locustodea for this fauna are the Decticidæ and the Phaneropteridæ: here we find 23 species belonging to the first named family, and 19 to the second. Among the Phaneropteridæ the flightless species are 15 in number; 16 species of Decticidæ are also flightless. It is not surprising, therefore, that we find many endemics in this district: 13 species are peculiar to it. Among these endemics there are no fewer than 6 species of *Pœcilimon*, all belonging to the group with non-denticulate cerci, which group presents one of the most characteristic features of the Balkano-Anatolian fauna having its centre of origin and distribution in this and in the neighbouring Armenian district. One species of *Isophya* (*I. paveli*) is also peculiar to Western Anatolia. Of Decticidæ two species of *Platycleis* (*P. truncata* and *P. schereri*), two *Olynthoscelis* (*Ol. signata* and *Ol. prasina*), *Drymadusa spectabilis*, and *Gampsocleis recticauda* are also Western Anatolian endemics. Considering all these endemics, it is noticeable that their specific features are very well marked and very constant, which gives us the evidence that these species are ancient and undoubtedly autochthonous forms. Thus we come to the conclusion that the Locustodean fauna of the Western Anatolia bears some peculiar features and is of great age. The composition of the other suborders of this fauna is of a rather mixed and indeterminate character.

As for the more recent elements of the Western Anatolian Orthopteran fauna, we may distinguish amongst them the forms of the Steppe fauna (*Stenobothrus* spp., *Stauronotus brevicollis*, etc.) which came here through the Balkan peninsula, and, what is more interesting, some species characteristic for the Western Mediterranean (Tyrrhenian) province, which are six in number, as follows: *Geomantis larvoides*, *Acrotylus longipes*, *Paracaloptenus caloptenoides*, *Platycleis nigrosignata*, *Olynthoscelis chabrieri*, and *Anterastes serbicus*. All of them, except *Acrotylus longipes*, are wingless and doubtless very ancient in their origin; the careful study of their distribution shows that it is discontinuous, which allows us to think that a connection between the Tyrrhenian and Balkano-Anatolian has been ancient also and ceased long ago.

The limits of this district are not yet sufficiently known to us. It is certain, however, that the north-western limit does not coincide with the recent natural limit of the Anatolia—with the Bosphorus and the Sea of Marmora, but it is to be looked for somewhere in the Balkanian peninsula. The Western Anatolian district occupies, conclusively, the more southern part of the last named peninsula, the western part of Anatolia from the Mediterranean Sea to the western borders of the interior Anatolian plateau, extending along the southern shore of the Black Sea as far eastwards as the neighbourhood of Trebizond.

5. *The Armenian district* (Ar.).

The whole number of species known from this district is larger than that of any other, being 134 (8 M + 62 A + 54 L + 10 G), which indicates the exceptional richness of its fauna.

The analysis of this fauna shows its affinity with the fauna of the preceding district, since 62 species are in common with the latter; it is of interest that many species are peculiar to both these districts, being unknown beyond their limits. This affinity is certainly due to the fact that they both belong to the same (Balkano-Anatolian) province. Far more interesting is the difference between them: out of 134 Armenian Orthoptera no fewer than 74 do not penetrate into Western Anatolia. This group is composed of very different elements. First of all we can distinguish in it an admixture of the more northern (steppe and boreal) forms, which are 12 in number, as follows:

Parapleurus alliaceus.
Stenobothrus fischeri.
„ nigromaculatus.
„ apricarius.
„ macrocerus.
„ hæmorrhoidalis.
Stenobothrus pulvinatus.
„ scalaris.
Gomphocerus sibiricus caucasicus.
Arcyptera fusca.
Locusta caudata kolenatii.
Olynthoscelis grisea.

The absence of these forms from Western Anatolia may indicate that they did not come to Armenia through the Balkanian peninsula but across the Caucasian isthmus. Some of them, for example *Arcyptera* and *Gomphocerus*, are absent from Western Anatolia simply because in this latter district there are no places (high mountains) suitable for their habitation. The same cause explains to us why the following four alpine species: *Orphania scutata zacharovi*, *Psorodonotus brunneri*, *Ps. fieberi*, and *Ps. specularis*, do not penetrate into Western Anatolia.

A very characteristic group of the Armenian Orthoptera is formed by the 13 species belonging to the true Eremian fauna. Their list is as follows:

Eremiaphila genei.
Acrida robusta.
Stenobothrus simplex.
Stauronotus anatolicus.
Pallasiella truchmana.
Pyrgodera armata.
Œdaleus mlokosiewitchi.
Sphingonotus balteatus.
Sphodromerus cœlosyriensis.
Platycleis escalerai.
Medecticus assimilis.
Gryllus tartarus obscurus.
„ hebræus.

Since all these species are good flyers it is evident that they came into Armenia in recent times from the neighbouring deserts of Persia and Mesopotamia; this view is supported by the fact that most of them are restricted to the eastern parts of the Armenian district.

But the majority in the group of Armenian Orthoptera which do not reach Western Anatolia belong to species peculiar to Armenia (or to both Armenia and Syrian Anatolia). They are 23 in number, as follows :

Stauronotus hauensteini kurda.
*Cuculligera maculinervis.
*Pamphagus yersini.
* „ brunnerianus.
*Eunothrotes derjugini.
Pœcilimonella armeniaca.
Pœcilimon tschorochensis.
„ kutahiensis.
„ syriacus.
„ concinnus.
*Kurdia nesterovi.
*Phonochorion satunini.
Isophya rodsjankoi.
* „ poltoratskyi.
Saga cappadocica.
*Drymadusa curvicercis.
* „ recticauda.
* „ konowi.
*Olynthoscelis annulipes.
* „ signata.
* „ zebra.
„ kurda.
*Troglophilus escalerai.

No fewer than one half of them should be regarded as the relics of the "ancient Mediterranean" fauna (these are marked with an asterisk), to which also belong the following 13 species whose area of distribution extends also beyond Armenian limits, as they are to be found in the neighbouring districts of Aderbeidzhan, Caspian Transcaucasia, and Somkheto-Kakhetia :

Œdipoda schochi schochi.
Thalpomena ledereri.
Heliopteryx humeralis.
Tmethis saussurei.
„ carinatus.
„ cisti.
„ bilobus.
Tmethis escherichi.
„ holtzi.
Nocarodes serricollis.
Pezotettix rugulosa.
Platycleis squamiptera.
Paradrymadusa sordida.

We find, thus, in Armenia 27 relics of the "ancient Mediterranean" fauna which find here their western limit of distribution and do not reach Western Anatolia.

The remaining 7 species of Armenian Orthoptera which do not range farther westwards (*Empusa pennicornis*, *Acrida nasuta*, *Isophya triangularis*, *I. acuminata*, *Olynthoscelis indistincta*, *Dolichopoda euxina*, and *Gryllus frontalis*) are partly of indeterminate zoogeographical value, or their absence from Western Anatolia may be explained as a result of insufficient investigations.

Summarizing the results of our analysis of the Armenian fauna we may conclude that it is a Balkano-Anatolian fauna in its chief characters but well distinguished from it by (1) the well expressed influence of the Eremian fauna, (2) the great number of endemics and relics of the "ancient Mediterranean" fauna, and (3) some admixture of boreal and steppe forms.

I think the frontiers of the Armenian district should be drawn in the following manner.

The northern boundary coincides with the chain of Pontus, coming on the east very near to Batoum and embracing a narrow strip of the Adzharian chain; from here it runs southwards along the Arsian chain as far as Arax, where the contact of Armenian and Aderbaidzhan fauna takes place; farther on the boundary turns eastwards along the chain of Aghridagh as far as Ararat, from where it goes southwards along the watershed of the basins of Urmiah and Tigris. The western boundary is presented by the margin of the central plateau of Anatolia, and the southern one goes in its western part along the Cilician Taurus and Antitaurus, not yet being satisfactorily known farther eastwards owing to the lack of investigation. I suppose it coincides with the Armenian Taurus.

As the territory of this district is far more extensive than that of any other, it causes us to suppose that it should be divided into two or more separate districts. Some modifications of the Orthopteran fauna of different parts of Armenia support this conclusion, but I cannot offer any satisfactory division, as our knowledge of the fauna of southern and south-eastern parts of Armenia is extremely limited. Further investigations of this district should be, therefore, of the greatest zoogeographical interest.

6. *The Syrian Anatolia* (**A.S.**)

This district belongs to those which have been less investigated, as is evident from the small number of species known of it, this being only 106 (9 M+50 A+38 L+9 G), though its southern position and dry climate offer the best conditions for the development of the richest Orthopteran fauna.

As for the composition of its fauna, it may be regarded as very closely related to the fauna of Syria proper, all differences being of an accidental nature. On the contrary, the difference existing between this fauna and that of Armenia is rather well defined in the lack of the most characteristic Armenian endemics and in the evident influence of the Eremian fauna which is a typical feature of the fauna of Syria.

The boundary between this district and the Armenian one coincides with the southern limit of the latter district following the chain of the Cilician Taurus; along the Euphrat valley this district penetrates into Armenia, as is to be seen on the map. All the other boundaries of this district lie beyond the limits of the country which we are studying now and are entirely unknown as yet.

7. *The Pontian district* (**P.**).

The fauna of this district includes 59 species of Orthoptera (1 M+27 A+20 L+11 G); having been well investigated it cannot be considered very rich.

The analysis of the Pontian fauna shows us that it is very closely related to the fauna of Western Anatolia, including only

15 species which do not range into the latter district. Of these 15 species no fewer than three or four (*Gryllus frontalis*, *Stenobothrus macrocerus*, *Arachnocephalus vestitus* and, perhaps, *Dolichopoda euxina*) should be regarded as not having been found as yet in Western Anatolia owing to the lack of investigations only; one—*Œdaleus mlokosiewitchi*, being a very strong flyer, doubtless came to the Pontian district from the east in recent times; the presence of *Œdipoda schochi schochi* may be satisfactorily explained by the influence of the neighbouring Armenia; and, finally, three species are peculiar to the Pontian district—*Podisma koenigi* (Pontian endemic ranging also into the adjacent western portion of the Somkheto-Kakhetian district), *P. satunini*, and *Olynthoscelis kerketa*. The remaining six species are of great interest: three of them are definitely boreal in their origin and inhabit the alpine district of Western Caucasus, from whence they come into the Pontian district; this descendance of the representatives of alpine fauna to the sea-level is due to the great humidity of the Pontian climate, this fact being very characteristic for the fauna of this district. The last three species are *Pœcilimon schmidti*, *Isophya pyrenæa*, and *Olynthoscelis fallax* —all northern Balkanian in their origin and sylvan in their habitation, which leads us to the conclusion that they come to the Pontian district from the north—through the Crimea.

Thus, we may consider the Pontian fauna as an impoverished Balkano-Anatolian one, with the admixture of peculiar and boreal forms and species of northern Balkanian origin which came here from the north.

The eastern limit of the Pontian district is formed by the chain of Suram; the southern boundary goes along the Adzharo-Imeretian chain, approaching the Black Sea near Kobulety and turning from here westwards along the chain of Pontus; the western boundary is rather obscure and is to be looked for somewhere near Trebizond; the north-eastern boundary coincides with the upper limit of the forests on the Western Caucasus; and the north-western separating the Pontian district from that of Novorossiisk is indefinite, as we shall see later on.

8. *The Novorossiisk district* (N.).

This district is one of the less investigated ones, the whole number of Orthoptera known from it being 50 (4 M+21 A+18 L+7 G).

Analysing its fauna we observe the very close resemblance of it to that of the South Russian steppe fauna and, on the other hand, to that of the Pontian district. This intermediate character of the Novorossiisk fauna is to be explained by the geographical position of the Novorossiisk district between the steppe of South Russia and the district of Pontus. The differences of the Novorossiisk fauna from that of the South Russian steppes are expressed in seven species, three of them being boreal in their origin (*Stenobothrus scalaris*, *Psophus stridulus*, and *Olynthoscelis* *griseoaptera*) and penetrating hence from the mountains of Western Caucasus; one (*Platycleis sepium*) is a Balkano-Anatolian species coming from the Pontian district; and three remaining ones (*Parameles taurica*, *Olynthoscelis pontica*, and *Pezotettix giornai*) are of special interest. The first two of them are peculiar to the southern part of the Crimea, and the *Pezotettix* is a characteristic Mediterranean species, unknown as yet in the Crimea, though doubtless present there. The presence in the Novorossiisk district of these three species, which are absent from all other districts of the Caucasus, indicates that this district was once in a direct connection with the south of the Crimean peninsula, the time and place of this connection being at present unknown to us.

As to the boundaries of the Novorossiisk district, its intermediate position and the transitional character of its fauna render them very obscure; I think they are not very markedly defined; its southern boundary separating it from the Pontian district is to be looked for somewhere between Tuapse and Sotchi.

9. *The Somkheto-Kakhetian district* (S.-K.).

The Orthopteran fauna of this extensive district, though fairly well investigated, is not yet fully known, as is evidenced by the fact of the recent description of some new species and subspecies inhabiting it. The whole number of the known Somkheto-Kakhetian Orthoptera reaches 79 (7 M + 35 A + 24 L + 13 G), which should be less than the real number by some 10–12 forms.

The first problem to be solved is whether this district belongs to the Steppe or to the Balkano-Anatolian province. Let us consider its affinities to both of them.

This district has in common with the Steppe province (districts of Southern Russia and of Kuban-Terek) 69 species, the difference being 21. Temporarily setting aside eight Somkheto-Kakhetian endemics, the remaining 13 are as follows:

*Empusa pennicornis.
*Tettix depressa.
*Paratettix meridionalis.
*Thalpomena ledereri.
*Pœcilimon distinctus.
* „ bosphoricus.
*Isophya adelungi.
*Isophya pyrenæa.
* „ amplipennis.
* „ acuminata.
*Paradrymadusa sordida.
Nemobius heydeni.
Gryllus lateralis.

No fewer than eleven of these (marked with an asterisk) are Balkano-Anatolian species or belonging to the characteristic Balkano-Anatolian genera, and two Gryllids only are recent invaders from the adjacent deserts of the Caspian Transcaucasia. Thus it is evident that the difference between the Somkheto-Kakhetian and the Steppe fauna is very well expressed and indicates the entirely different sources of their origin.

Turning to the relation of the Somkheto-Kakhetian fauna to the Balkano-Anatolian one we see, that only 16 species inhabiting this district are foreign to other districts of the Balkano-Anatolian province, eight of them being peculiar Somkheto-Kakhetian forms. The remaining eight species are:

Stenobothrus lineatus.
Pœcilimon distinctus.
Isophya adelungi.
„ pyrenæa.
Platycleis vittata.
Olynthoscelis fallax.
Nemobius tartarus.
Gryllus lateralis.

Out of these only *Stenobothrus lineatus* and *Platycleis vittata* may be regarded as proofs of the influence of the steppe fauna; two Gryllids are of desert origin; and all others belong to the Balkano-Anatolian genera.

The above is sufficient to enable us to come to the conclusion that this district may be regarded as a part of the Balkano-Anatolian province, a conclusion confirmed by the study of the Somkheto-Kakhetian endemics. They are eight in number, as follows:

Arcyptera flavicosta transcaucasica.
Celes variabilis carbonaria.
Tmethis zaitzevi.
Nocarodes rimansonæ.
Podisma koenigi (peculiar to this and Pontian district).
Isophya bivittata.
Leptophyes nigrovittata.
Olynthoscelis distincta.

All these peculiar forms, with the exception of *Arcyptera*, *Podisma*, and *Celes*, belong to the Balkano-Anatolian genera, and are doubtless not recent invaders. This strongly supports my opinion as to the affinities of the Somkheto-Kakhetian district. *Podisma koenigi* presents an evidence of the influence of the Pontian fauna, and two peculiar characteristic steppe species, *Arcyptera flavicosta* and *Celes variabilis* (as well as *Stenobothrus lineatus* and *Platycleis vittata*), are doubtless immigrants from the Kuban-Terek district (through the Daghestan), the somewhat different natural conditions of Transcaucasia causing the subspecific differences between the Transcaucasian and the primary steppe forms.

We ought, therefore, to consider the Somkheto-Kakhetia as a district of the Balkano-Anatolian province, bearing in its fauna some hints of an influence of the South Russian steppe fauna, migrating from the north around the eastern end of the Caucasus through the Daghestan.

The outlines of the Somkheto-Kakhetian district are very complicated and circuitous. I include in it the southern forest-clad slopes and hills of the Great Caucasus from Svanetia on the west to the south-eastern extremity of this chain: here the district branches around this end on the northern slopes, thus coming in contact with the Daghestanian district; through the Suram meridional chain the northern half of the Somkheto-

Kakhetian district is connected with the southern part, the district thus ranging all over the northern slopes of Minor Caucasus as far eastwards as Karabagh, where its fauna, becoming gradually poorer, comes in contact with the fauna of Aderbaidzhan.

10. *The Talysh district* (T.).

The fact that we only know 45 species of Orthoptera (3 M + 24 A + 8 L + 10 G) from this district is certainly due not to its poverty but to incomplete investigations.

As regards the composition of the Talysh fauna, it gives the impression of bearing resemblance to that of the adjacent Caspian Transcaucasia, being distinguished from it by the presence of five forms only, as follows:

Acrida turrita turrita.
Parapleurus alliaceus.
Stenobothrus macrocerus.
Epacromia strepens strepens.
Platycleis capitata.

The latter of these is an endemic species, while the presence of the four remaining ones indicates the close affinity of the Talysh fauna to that of the Balkano-Anatolian province. The most remarkable fact is that *Acrida turrita* and *Epacromia strepens* are represented in the Talysh district, not by the desert subspecies inhabiting the Caspian Transcaucasia and Aderbaidzhan, but by the same races that are met with in the districts belonging to the Balkano-Anatolian province, the range of these subspecies being discontinuous. The affinity of the Talysh fauna with the Balkano-Anatolian one is even more defined by the fact that its difference from the latter can be based upon a single subspecies (leaving the endemic *Platycleis capitata* aside)—*Decticus verrucivorus boldyrevi*, which no doubt came here recently from the neighbouring deserts. The influence of the Eremian fauna on the fauna of Talysh is, generally speaking, very well marked, resulting in the presence of such forms as *Thisoecetrus dorsatus*, *Platycleis escalerai*, *Liogryllus bimaculatus*, etc., but it should be regarded as of secondary nature. The immediate connection of the Talysh with the other districts of the Balkano-Anatolian province is now absent, but it no doubt existed formerly; I think it should be looked for in the south-eastern (Karabaghian) branch of the Somkheto-Kakhetian district which formerly used to reach the Talysh.

In the district of Talysh I include only the rather narrow strip along the southern shore of the Caspian Sea, the southern boundary of this district being the upper limit of the forests on the northern slopes of the Talysh mountains. The north-western boundary delimitating Talysh from the adjoining deserts of Caspian Transcaucasia is rather indefinite; the north-eastern one is completely unknown.

11. *The district of Aderbaidzhan* (Ad.).

This district possesses a very rich Orthopteran fauna, the number of species known being 125 (9 M + 1 P + 76 A + 24 L + 15 G); the real number should be considerably larger, not less, I believe, than 150–160.

The most interesting features of this fauna are as follows. First of all, the presence of a representative of the suborder Phasmodea (*Gratidia bituberculata*)—which is not to be met with in any other district, except Caspian Transcaucasia—clearly indicates that the Aderbaidzhan fauna belongs to a quite distinct zoogeographical division. This is supported by the large number of Mantodea, Acridiodea, and Gryllodea, while the number of Locustodea is comparatively small. Among the Acridiodea the large number of species belonging to the family Œdipodidæ is very conspicuous; there are thirty Œdipodids here against ten, for example, inhabiting the neighbouring Somkheto-Kakhetian district. But the fauna of Aderbaidzhan is as remarkable for what it lacks as for what it possesses. Out of these negative features the total absence of the genera *Chrysochraon*, *Gomphocerus*, *Arcyptera*, *Psophus*, *Celes*, and *Podisma* is very remarkable; they are all of northern (boreal or steppe) origin, and do not reach this district. Yet more interesting is the composition of the fauna of Locustodea: out of the whole family Phaneropteridæ, so well represented in the districts belonging to the Balkano-Anatolian province, we only find two here—*Phaneroptera falcata* and *Tylopsis thymifolia*, both very strong flyers and doubtless recent immigrants; the highly characteristic for the Balkano-Anatolian fauna family Sagidæ is represented in Aderbaidzhan by one species only, the most widely distributed *Saga ephippigera*; the majority of Locustodean fauna being thus formed by the Decticidæ, which are sixteen in number, mostly species of distinct "ancient Mediterranean" origin.

The originality of the Aderbaidzhan fauna is most clearly demonstrated by the large number of peculiar species (some of them also ranging into Caspian Transcaucasia); nearly one third of them are not to be found in any other district of the country, being distributed beyond its limits, while eighteen are true endemics, as follows:

Eremiaphila persica.
Brunnerella mirabilis.
Scintharista brunneri.
Thalpomena persa.
Helioscirtus moseri tichomirovi.
Tmethis persa.
„ carinatus.
Nocarodes woronowi.
„ schelkovnikovi.

Derocorys roseipennis lazurescens.
Drymadusa grisea.
Paradrymadusa pastuchovi.
„ satunini.
„ persa.
„ longipes.
„ bocquilloni.
Platycleis persica.
Olynthoscelis satunini.

Amongst these endemics a great percentage of the "ancient Mediterranean" forms is evident, as, for example, all *Paradrymadusa* species, *Drymadusa grisea*, two species of *Nocarodes*, etc.

Very characteristic of the Aderbaidzhan fauna are also numerous Eremian genera and species, for example: *Eremiaphila*, *Oxythespis*, *Helioscirtus*, *Sphingonotus*, *Derocorys*, *Sphodromerus*, etc.

Summarising the results of our analysis, we may characterise the fauna of the Aderbaidzhan district as a true Eremian one, with a well-marked admixture of "ancient Mediterranean" forms and with very slight indications of the steppe fauna, which penetrates here through the Somkheto-Kakhetian and Armenian districts.

I include in the Aderbaidzhan district the Persian province bearing this name (but not the recently formed republic of Azerbaidzhan in Transcaucasia), as well as the valley of middle Arax from Kaghyzman as far as Migry. Thus, the northern boundary is to be drawn along the southern slopes of the Minor Caucasus at a somewhat considerable height, about 6000–7000 feet above the sea-level. To this district also belongs (I am not yet sure whether partly or wholly) the Karabagh, where the Aderbaidzhan fauna comes in direct contact with the here already impoverished Somkheto-Kakhetian one. Farther eastwards the northern boundary of Aderbaidzhan goes along the eastern boundary of the Zangezur chain and near Migry goes over the Arax, turning eastwards nearly parallel with the latter river along the chain of Karadagh as far as the Talysh chain; farther on the boundary of Aderbaidzhan coincides with the latter chain. The western boundary is the same as the eastern limit of Armenia, which we have already considered above. As for the southern limit it is as yet unknown, but there are some indications that it lies rather far southwards in Central Persia.

12. *The district of Caspian Transcaucasia* (**T.C.**).

The Orthopteran fauna of the deserts of the eastern or Caspian Transcaucasia as compared with other districts has been more fully investigated. The amount of its known species is 98 (6 M + 1 P + 50 A + 24 L + 17 G), which number is, I suppose, very near to the real one.

If we take into consideration the uniformity of this district, its fauna may be regarded as a rather rich one, though poorer than that of Aderbaidzhan. The difference between the fauna of the latter district and that of Caspian Transcaucasia appears to be a very marked one, since as many as 45 Aderbaidzhanian forms do not reach Caspian Transcaucasia. Out of them 23, that is nearly half, are species of "ancient Mediterranean" origin, as follows:

Pallasiella bolivari.
Pyrgodera armata.
Brunnerella mirabilis.
Heliopteryx humeralis.
Charora crassivenosa.
Trinchus schrenki.
4 species of Tmethis.
4 species of Nocarodes.
Drymadusa grisea.
,, konowi.
4 species of Paradrymadusa.
Platycleis persica.
,, squamiptera.
Olynthoscelis satunini.

The typical Eremian forms which do not penetrate into Caspian Transcaucasia from Aderbaidzhan are 19 in number:

Eremiaphila persica.
Oxythespis wagneri.
Fischeria baltica.
Blepharis mendica.
Duronia fracta fracta.
Platypterna tibialis.
Scintharista brunneri.
Helioscirtus moseri moseri.
„ „ tichomirovi.
6 species of Sphingonotus.
Leptoternis gracilis.
Derocorys roseipennis lazurescens.
Schistocerca peregrina.
Sphodromerus serapis.

This list includes a rather large percentage of forms of more southern origin (*i. e.* Indo-Ethopian), such as *Oxythespis*, *Fischeria*, *Blepharis*, *Schistocerea*, *Sphodromerus*, which are to be regarded as recent invaders into the Eremian subregion and do not reach its northern parts, which accounts for their absence from the Caspian Transcaucasia. Besides, two species are common to the latter district but represented by distinct subspecies (*Duronia fracta* and *Derocorys roseipennis*), and nearly all the remaining species are remarkable for their sporadic distribution, being bound to certain habitations which are not to be met with in Caspian Transcaucasia; their absence from the latter district is thus easy to understand.

The remainder is formed of three species: *Stenobothrus zubowskyi*, *Callimenus dilatatus*, and *Orphania scutata zacharovi*. The first of them is too little known as regards its geographical distribution, and the two others are Balkano-Anatolian species confined to the alpine pastures which are absent from Caspian Transcaucasia.

The negative features which distinguish the fauna of Caspian Transcaucasia from that of Aderbaidzhan are thus very numerous. Nevertheless, they are but of little zoogeographical value, being due to the comparative youth of the fauna of Caspian Transcaucasia, it being the cause that "ancient Mediterranean" species (mostly flightless or bad flyers) and the Eremian ones of more southern origin have not had time enough to extend their range of distribution into this district but recently left by the waters of the Caspian Sea.

Let us see now what is the positive distinction of the fauna of Caspian Transcaucasia from that of Aderbaidzhan. The forms of Caspian Transcaucasia which are not found in Aderbaidzhan are 19 in number, as follows:

Gelastorrhinus sagitta.
Duronia fracta kalmyka.
Stenobothrus petræus.
* „ parallelus.
*Gomphocerus maculatus.
*Arcyptera flavicosta transcaucasica.
*Celes variabilis carbonaria.
Derocorys roseipennis roseipennis.
**Pœcilimon distinctus.
** „ bosphoricus.
**Isophya adelungi.
** „ schmidti.
**Leptophyes albovittata.
**Paradrymadusa sordida.
Platycleis burri.
„ decticiformis.
* „ vittata.
* „ grisea.
**Olynthoscelis indistincta.

Two of them belong to the species represented in Aderbaidzhan by other races (*Duronia* and *Derocorys*), and four are of no value, their zoogeographical character being unknown (*Gelastorrhinus*, *Stenobothrus petraeus*, *Platycleis burri*, and *Pl. decticiformis*). Thus, the difference is based on 13 species only, out of which six (marked in list with an asterisk) belong to the steppe fauna and seven (marked with two asterisks) are Balkano-Anatolian; they all inhabit the Somkheto-Kakhetian district as well, which explains their appearance in Caspian Transcaucasia through recent immigration from the latter district.

This connection with the Somkheto-Kakhetian fauna is, nevertheless, but of little importance, the differences between it and that of Caspian Transcaucasia being too numerous.

Summarizing these facts, we may conclude that the Orthopteran fauna of the Caspian Transcaucasia is undoubtedly in close affinity with the Aderbaidzhan fauna, being nothing more than the northern vanguard of the latter, distinguished by some impoverishment and by slight marks of an influence from the Somkheto-Kakhetian fauna. The past history of the fauna of Caspian Transcaucasia should be rather short and simple: the vast plains of eastern Transcaucasia dried up after the retreat of the Caspian Sea were populated by the most mobile and progressive elements of the Aderbaidzhan fauna, while Balkano-Anatolian and steppe forms proved mostly to be unadaptable to the rough conditions of life in the newly formed deserts.

The southern boundary of this district, delimitating it from Aderbaidzhan, is not clearly enough defined, the still continuing northward migration of Eremian elements being the cause of its indistinctness; the approximate direction of this boundary is to be seen above in the section dealing with the Aderbaidzhan district (p. 466).

The boundaries between the Caspian Transcaucasia and the Somkheto-Kakhetian district are also mentioned above. The district of Caspian Transcaucasia gives a very long and narrow branch northwards, along the western shore of the Caspian Sea, but it is still uncertain where the northern boundary is to be drawn, for the deserts along this shore are as yet unexplored.

13. *The district of Caspian Ciscaucasia* (C.C.).

This district is inhabited by 70 species of Orthoptera (4 M + 39 A + 13 L + 14 G) and, as its fauna may be regarded as having been thoroughly investigated, this number cannot be expected to increase in a marked degree after further explorations.

A glance at the composition of this fauna enables us to conclude that it belongs to the Eremian subregion. This is evident from the fact of the relative abundance of Acridiodea and Gryllodea in comparison with the poverty of Locustodea; it is even still more supported by the study of families: Œdipodidæ being well represented, the Decticidæ also, while of the Phaneropteridæ there is here one species only—the very well-flying *Phaneroptera falcata*, penetrating into this district from the neighbouring district of Kuban-Terek along the valley of Kuma.

The fauna of Caspian Ciscaucasia shows the greatest resemblance to that of the district of Caspian Transcaucasia, the difference between them being based upon the negative features of the first, while a rather large number (46, *i. e.* 2 M + 1 P + 21 A + 17 L + 5 G) of Transcaucasian Orthoptera do not range into Ciscaucasia; a careful examination of this group shows that it is composed of species of distinct southern origin, except *Arcyptera flavicosta* and *Celes variabilis*, which are members of the steppe fauna represented in Transcaucasia and Ciscaucasia as well though by different geographical races. As for the positive differences of the Ciscaucasian fauna from that of Caspian Transcaucasia they are 16 in number, as follows:

Acrida turrita turrita.
*Chrysochraon dispar.
*Stenobothrus hæmorrhoidalis.
*Stauronotus brevicollis.
* „ kraussi.
Arcyptera flavicosta flavicosta.
*Epacromia tergestina.
Celes variabilis variabilis.
Œdipoda schochi caucasica.
**Hyalorrhipis clausi.
Tmethis muricatus.
*Saga pedo.
*Platycleis montana.
Decticus verrucivorus schugurovi.
**Gryllus odicus.
**Tridactylus tartarus.

Five of them are but geographical races (subspecies) of the species represented in Transcaucasia as well; one, *Tmethis muricatus*, is very closely related to the southern *T. bilobus*, and is, perhaps, also but a race of the latter. The remaining group of ten species is composed of seven steppe forms (marked in above list with an asterisk) and three are desert species originating from the Turanian province of the Eremian subregion (two asterisks). The presence of these latter is very interesting, as it gives an evidence of the affinity of the Ciscaucasian fauna to that of the Kirghizian district of the Turanian province adjacent to it on the north-east. It is a very curious fact that the affinity of the Ciscaucasian fauna to the Turanian province is far closer than it is to the Iranian one; a comparison of the fauna of Caspian the Ciscaucasia with that of the Kirghizian deserts shows us that the first contains one species only which is not represented in the second: this is *Œdipoda schochi caucasica*, an evidently new intruder into the Ciscaucasian plains from the dry stony hills of Transcaucasia. This leads us to the conclusion that the desert plains of Caspian Ciscaucasia, quite recently left by the retreated Caspian Sea, got their Orthopteran fauna mostly from the north, being populated by the most progressive elements of the steppe and Turanian fauna (the greater part of which are also proper to the Iranian province of the same Eremian subregion), while the migration from Transcaucasian deserts was prevented by some unknown factors. As the eastern Ciscaucasian plains were at first separated from the Kirghizian deserts by the Strait of

Manytch (which joined the Black Sea to the Aralo-Caspian basin), it is necessary to conclude that the process of populating these plains began after the drying up of the above-named strait, and the whole fauna of the Caspian Ciscaucasia should be regarded as being of quite recent origin, which explains the absence of some characteristic Kirghizian forms, as, for example, *Armene alata*, *Oxythespis turcomaniæ*, *Pyrgodera armata*, etc. All above considerations support the idea that the deserts of the Caspian Ciscaucasia form a distinct zoogeographical district of the Turanian province.

As for the boundaries of this district, they are all well marked except the southern one. This district occupies the clay and sandy deserts adjacent to the lower currents of the rivers Kuma and Terek, as well as the whole valley of the Manytch. I consider the latter valley as the northern limit of this district, while the western and south-western are determined by the corresponding boundaries of the South-Russian and the Kuban-Terek districts. The southern boundary, delimitating this district from the Caspian Transcaucasia, is yet unknown, and I suppose it is not very sharply defined.

14. *The district of Western Caucasus* (C.Oc.).

The Orthopteran fauna of the subalpine and alpine zones of the western part of the main Caucasian chain includes 40 species (24 A + 13 L + 3 G). Amongst them a very striking group is formed by 20 species of evident boreal origin, as follows:

Tettix bipunctata.
,, subulata.
Parapleurus alliaceus.
Chrysochraon dispar.
,, brachypterus.
Stenobothrus nigromaculatus.
* ,, viridulus.
,, hæmorrhoidalis.
* ,, ventralis.
* ,, scalaris.
Stenobothrus apricarius.
*Gomphocercus sibiricus caucasicus.
Arcyptera fusca.
*Mecostethus grossus.
*Psophus stridulus.
*Podisma pedestris.
*Locusta caudata caudata.
*Platycleis rœseli.
*Decticus verrucivorus verrucivorus.
*Olynthoscelis griseoaptera.

The presence of these boreal species as well as the total absence of representatives of Mantodea, the small number of Gryllodea, the poverty of Œdipodidæ and Decticidæ—this all gives to this fauna a rather northern character. This character is further strengthened by the remarkable fact that eleven, *i. e.* more than half of the above-named boreal species (marked by an asterisk), show a discontinuous range of distribution, their main (northern) area being separated from the Caucasian one by a large space of South-Russian steppes from which these species are totally absent. As regards the way by which these boreal elements came to the Caucasus there may be two different suggestions: either they migrated via Balkania and Asia Minor, or reached the Caucasus direct from the north at some remote time when the climate of South Russia was colder and damper, which might occur during the Glacial period. As a good many of the boreal species, as for example, *Mecostethus*, *Psophus*, *Podisma pedestris*, are doubtless absent from Asia Minor, the latter supposition should be by far the more correct.

The remaining 22 Orthoptera of this district show rather mixed affinities. The most marked affinity is that to the Balkano-Anatolian fauna as expressed by the presence of *Nocarodes cyanipes*, four species of *Pœcilimon*, four *Isophya* and two *Psorodonotus*, while the direct influence of the steppe fauna is evidenced by the presence of such forms as *Stenobothrus macrocerus*, *St. parallelus*, and *Celes variabilis variabilis*.

The endemic forms of the Western Caucasus are only four in number: *Podisma satunini*, *P. rufipes*, *Isophya caucasica*, and *I. kalischevskyi*, their small number being a rather characteristic feature of this fauna.

The northern and southern boundaries of this district coincide with the upper limits of the forests on the corresponding slopes of the Caucasian chain; while the eastern boundary, delimitating Western Caucasus from the district of Eastern Caucasus, is as yet insufficiently known; I suppose it is somewhere near the sources of the Terek and the Aragva.

15. *The district of Eastern Caucasus* (C.Or.).

Only 17 species of Orthoptera (11 A + 5 L + 1 G) are known in the eastern part of the Caucasian chain; its fauna being thus far poorer in comparison with that of the preceding district. The most interesting features of this fauna are: the small number of boreal and, in general, northern species and, furthermore, the presence of two exceedingly well characterized and, therefore, very ancient endemics—*Podisma lezgina* and *Phlocerus menetriesi*, the latter being the single representative of its genus.

The boundaries of this district are easy to understand.

16. *The district of the Caucasus Minor* (C.M.).

The Orthopteran fauna of this district, being rather well investigated, includes but 52 species (30 A + 18 L + 4 G), which indicates its poverty.

The analysis of this fauna indicates its close affinity to that of Armenia, only twelve species being strange to the latter district, as follows:—

*Chrysochraon dispar.
Stenobothrus werneri sviridenkoi.
Gomphocerus variegatus.
*Arcyptera flavicosta transcaucasica.
*Psophus stridulus.
*Celes variabilis carbonaria.
Pœcilimon similis.
*Meconema thalassinum.
*Platycleis bicolor.
* ,, weseli.
,, iljinskii.
*Decticus verrucivorus verrucivorus.

The bulk of this group evidently belongs to species of boreal origin (marked in the list with an asterisk), some of them being the leading forms of the Boreal fauna (*Chrysochraon*, *Psophus*, *Meconema*); their presence here, together with their absence from the mountains of Armenia, allows us to conclude that they came here somehow from the Great Caucasus, perhaps by the transverse chain of Suram which joins the mountains of the Minor Caucasus to the main chain. In this characteristic admixture of boreal forms, as well as in the presence of two endemics (*Stenobothrus werneri sviridenkoi* and *Platycleis iljinskii*), I see the sufficient cause for separating this district from Armenia.

The district of Caucasus Minor occupies the high table-lands of Akhalkalaki, Kars, and Alexandropol, sending a narrow and long branch along the shores of the Goktcha Sea and, farther south-eastwards, along the chain of Zangezur. The northern boundary coincides with the upper limit of Somkheto-Kakhetian forests; the western goes along the Arsian chain; and the southern is exceedingly circuitous, being not yet satisfactorily explored.

The difficult task of drawing the accompanying map of zoogeographical districts has been undertaken in a most friendly way by P. I. Nagorny, and I avail myself of the opportunity of once more expressing my sincere gratitude to him.

EXPLANATION OF THE MAP.

Zoogeographical division of the Caucasus and Western Asia.
(Text-fig. 1, p. 454.)

PALÆARCTIC REGION.

I. Steppe subregion.

South-Russian Steppe province.

R.M. (Rossia meridionalis).—South-Russian district.
K.-T.—Kuban-Terek district.
D.—Daghestan district.

II. Mediterranean subregion.

Balkano-Anatolian province.

N.—Novorossiisk district.
P.—Pontian district.
S.-K.—Somkheto-Kakhetian district.
C.M.—District of the Caucasus Minor.
T.—Talysh district.
Ar.—Armenian district.
A.M. (Anatolia mediterranea).—Western Anatolian district.
A.S.—District of the Syrian Anatolia.

III. Eremian subregion.

1. *Iranian province.*

Ad.—Aderbaidzhan district.
T.C.—District of the Eastern (Caspian) Transcaucasia.

2. *Turanian province.*

C.C.—District of the Eastern (Caspian) Ciscaucasia.

IV. Caucasian subregion (?).

C.Oc.—(Caucasus occidentalis).—District of the Western Caucasus.
C.Or.—(Caucasus orientalis).—District of the Eastern Caucasus.

24. The Auditory Bulla and other Cranial Characters in the Mustelidæ. By R. I. Pocock, F.R.S., F.Z.S.

[Received March 22, 1921 : Read May 10, 1921.]

(Text-figures 14–18.)

CONTENTS.

	Page
Introduction	473
The Foramina in the Base of the Skull	474
The Internal Structure of the Auditory Bulla	478
The Classification of the Genera by the Bullæ	484

In 1869 (Proc. Zool. Soc. pp. 4–37) Flower described certain features in the base of the skull of several genera of Mustelidæ, especially those connected with the auditory bulla and the adjacent foramina, recording the position of the glenoid, carotid, and condyloid foramina, and noting the shape and relative prominence of the mastoid and paroccipital processes. In many instances he opened the bullæ and described the internal structure. The genera examined were *Lutra*, *Enhydris*, *Meles*, *Taxidea*, *Mephitis*, *Helictis*, *Arctonyx*, *Mydaus*, *Gulo*, *Mellivora*, *Galera*, *Martes*, *Mustela*, and *Rhabdogale* [=*Ictonyx*]. He summarised the results of his examination of the skulls of the Ursidæ, Procyonidæ, and Mustelidæ as follows:—(1) The cavity of the bulla is simple.... That is, although there are frequently trabeculæ or partial septa passing mostly transversely across the lower part, and generally connected with the tympanic ring, there is no distinct and definite septum dividing it into a separate outer and inner character [misprint for chamber]. (2) The paroccipital process is more or less triangular, and directed backwards, outwards, and downwards, standing quite aloof from the bulla. This relation depends chiefly on the want of development of the posterior portion of the bulla; and is absent, or obscure, in *Mustela* alone. (3) The alisphenoid canal is present in the true Bears and *Ailurus*; absent in all the others [*i. e.* in all Mustelidæ].

Although these statements have been copied over and over again in works on the classification of the Carnivora, further investigation shows that not one of them is exact. The bulla of *Helictis*, for example, is as completely divided as in the Felidæ, and there is a very distinct partition in *Grison*, *Gulo*, *Mellivora*, and other genera, although it is not so complete as in the typical Æluroidea. As regards the paroccipital process, although its prominence and remoteness from the bulla are well marked in such genera as *Lutra*, *Mephitis*, *Mellivora*, *Meles*, *Taxidea*, and others, it is in *Helictis* and *Grison* as closely applied to the posterior end of the bulla as in typical Felidæ, and it is even more confluent with the bulla in *Pœcilictis* than in

Mustela. Flower's statement about the absence of the alisphenoid canal may stand with the qualification that the canal may be retained as an abnormality.

In 1885, Mivart (Proc. Zool. Soc. pp. 363–389) supplemented Flower's observations with a few additional facts and included *Conepatus*, *Pœcilogale*, and *Lyncodon* in the list of genera.

Since that date it does not appear that the facts have been re-examined. The observations contained in the following pages, based mainly on specimens that have died in the Society's Gardens, may, therefore, be interesting and useful.

The Foramina in the Base of the Skull.

The Alisphenoid Canal.—This tube, as is well known, is typically absent in the Mustelidæ. But in one example of *Lutra lutra*, I find the remnants of it on the left side of the skull although the right side is normal. A little distance in front of the *foramen ovale* and higher up there is a small orifice through which a bristle can be passed so as to appear in the aperture common to the *foramen lacerum anticum* and the *foramen rotundum*. The passage is no doubt the homologue of the alisphenoid canal in the Canidæ, Ursidæ, *Ailurus*, Mungotidæ, etc. Except as an item of evidence supporting the view that the canal in question is a primitive Carnivore feature, the discovery of it in a skull of *Lutra* is of no great moment. As I have elsewhere pointed out, it may be present or absent in the Hyænidæ (Proc. Zool. Soc. 1916, p. 444, fig. 2).

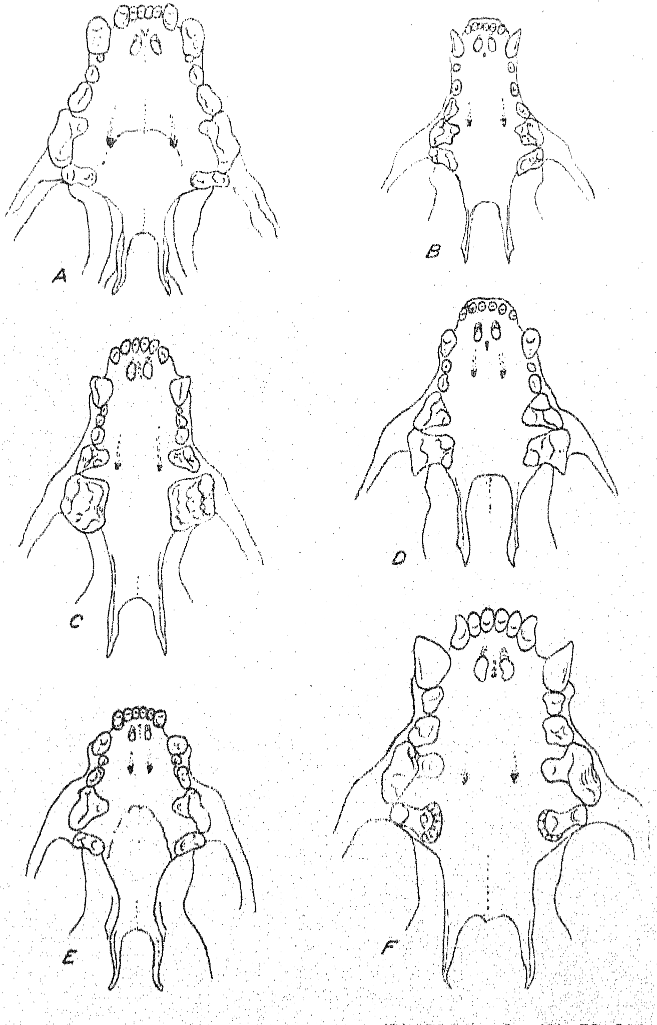
The Posterior palatine foramina.—The normal position of these is approximately opposite the inner lobe of the upper carnassial tooth (*pm.*^{1}) on the maxillo-palatine suture, along which they move to a certain extent backwards or forwards. They hold this position in *Martes*, *Charronia*, *Gulo*, *Tayra*, *Mellivora*, *Meles*, *Arctonyx*, *Mydaus*, and *Helictis*. In *Taxidea* they may be as far back even as the anterior edge of the molar. In *Lyncodon*, *Grison*, *Ictonyx*, *Pœcilictis*, *Lutra*, *Pœcilogale*, *Vormela*, and *Mustela*, with its related generic and subgeneric forms, *Gale*, *Putorius*, *Lutreola*, they are on the maxilla approximately opposite *pm.* 3 and removed from the maxillo-palatine suture. In *Mephitis*, *Spilogale*, and *Conepatus* they may be even nearer still to the anterior palatine foramina, opposite *pm.* 2.

It may be noticed that in all the genera with long jaws like *Meles*, *Arctonyx*, *Mydaus*, *Helictis*, and *Martes* they are set back on the suture, whereas in some genera with short jaws and often reduced dentition, like *Mustela*, *Vormela*, *Grison*, and *Lutra*, they are set forwards, wholly on the maxilla. Nevertheless this position is not always correlated with the length of the jaws and teeth, since they occupy the backward position in *Mellivora* and *Taxidea*.

Their variation in position within the Mustelidæ is interesting in view of their constancy in position in other families of

Carnivora. In the Ursidæ, Procyonidæ, Canidæ, and Felidæ they are always placed back upon the suture, whereas in the Hyænidæ,

Text-figure 14.



Palates of *Gulo gulo* (A), *Helictis everetti* (B), *Meles meles* (C), *Mephitis* sp. (D), *Grison* (E), *Mellivora ratel* (F), showing the position of the post-palatine foramina.

Mungotidæ, and the large number of genera usually assigned to the Viverridæ they open on the maxilla in front of the suture;

and in connection with the Æluroid (or Mungotoid) families cited, it may be noted that the Felidæ, which, like *Mustela*, *Grison*, etc., have shorter jaws and the teeth more reduced numerically than in any other Carnivora, they are set back, whereas in such relatively long-jawed forms as the typical Viverridæ they are wholly maxillary in position.

The Foramen rotundum.—As in the Canidæ, this foramen is visibly separated from the foramen lacerum anticum in profile view of the skull in *Martes*, *Charronia*, *Gulo*, *Helictis*, and *Taxidea*; but in *Mustela*, *Putorius*, *Grison*, *Lyncodon*, *Tayra*, *Ictonyx*, *Pœcilogale*, *Mellivora*, *Meles*, *Mephitis*, and *Lutra* it is at most visible as a separate orifice when the orbit is looked into from the front, lying quite close to the *foramen lacerum anticum* in a depression common to the two. Not uncommonly the two orifices are confluent owing to the failure of the partition to ossify, but within the limits of the genus *Ictonyx* there is individual or racial variation in this particular, and no doubt the same is true of other genera.

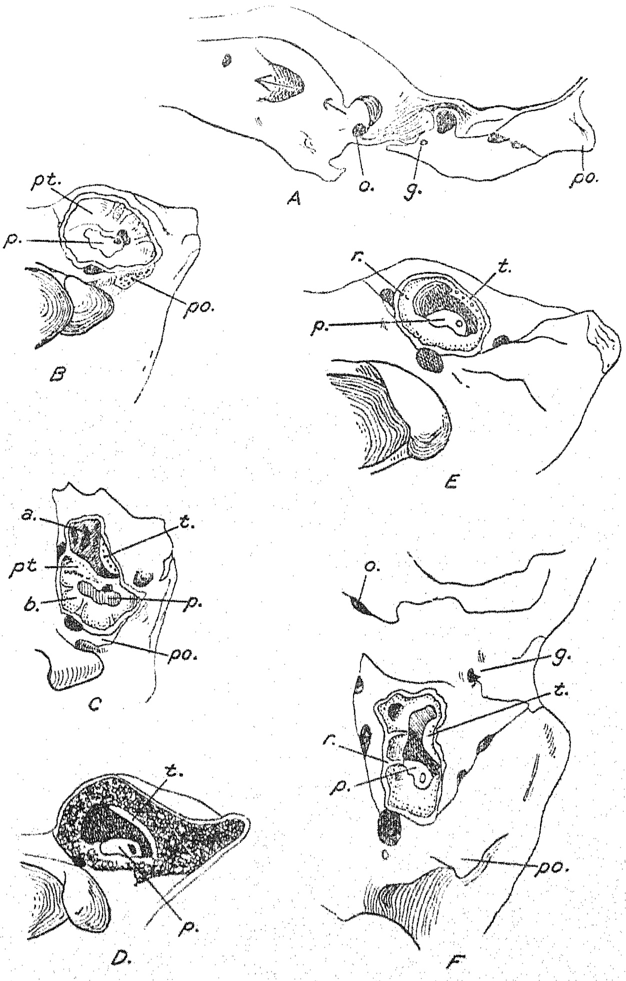
The Foramen ovale.—The position of this foramen with regard to the orifice of the eustachian tube varies in accordance with the length of the back of the skull and with the inflation of the anterior part of the bulla. Typically it is separated by a considerable space from that orifice as in *Mustela*, *Putorius*, *Martes*, *Charronia*, *Gulo*, *Tayra*, *Grison*, *Mellivora*, *Meles*, *Helictis*, and *Lutra*; but in *Ictonyx*, *Pœcilictis*, *Taxidea*, *Mephitis*, *Spilogale*, and *Conepatus* the foramen is only separated from the eustachian orifice by a thin plate of bone.

The Glenoid foramen.—The typical position of this in profile view of the skull is in front of the external auditory meatus either in line with it or slightly higher or lower as the case may be. It is lowest in *Taxidea*, where it is almost below the lower edge of the meatus. In *Meles* it is, on the contrary, almost above the upper edge of the meatus. In *Mustela*, *Martes*, *Charronia*, *Gulo*, *Tayra*, *Mellivora*, *Ictonyx*, *Grison*, and *Lutra* it holds intermediate positions. In *Mephitis*, *Spilogale*, and *Conepatus* it is, however, set right over the middle of the upper rim of the meatus; and in *Helictis* it occupies almost the same position—farther back even than in the Canidæ.

When the skull is viewed from below, the position of the foramen also varies with respect to the auditory meatus. In *Helictis*, *Mephitis*, *Spilogale*, and *Conepatus* it is quite concealed behind the rim of the orifice. In *Martes*, *Charronia*, and *Meles* it is just concealed by its anterior rim. In *Mustela*, *Putorius*, *Tayra*, *Ictonyx*, *Grison*, *Taxidea*, and *Mellivora* it is just visible in front of the anterior rim of the orifice. In *Gulo* and *Lutra* it is exposed in front of the tubular meatus, nearly as far inwards as in the Ursidæ.

The Stylomastoid foramen.—Typically this foramen lies on the inner side of the mastoid prominence and between it and the inflated portion of the bulla. It is approximately in line with

Text-figure 15.



A. Part of the skull of *Lutra lutra* showing the abnormal occurrence of the alisphenoid canal indicated by arrow.

B. Bulla of *Helictis everetti*, the posterior chamber opened from behind showing the partition (*pt.*) descending to the petrous.

C. The same from below cut open to show the partition (*pt.*) running obliquely between the anterior chamber (*a*) and the posterior chamber (*b*).

D. Bulla of *Putorius putorius* opened from behind, showing the thickened spongy tissue of the walls and the undivided cavity.

E. Bulla of *Lutra lutra* showing the partial division of the cavity by rafters.

F. The same from below.

Lettering :—*a*, *b*, anterior and posterior chambers of cavity (in B, C); *g*, glenoid foramen; *o*, foramen ovale; *p*, petrous portion of periotic; *po*, paroccipital process; *pt*, partition (in B, C); *r*, rafter; *t*, edge of tympanic annulus.

the glenoid foramen and some distance from the *foramen lacerum posticum*. Its position varies in accordance with the inflation of the bulla, and every gradation can be traced from *Mustela*, where it is thrust far out, to *Gulo*, *Lutra*, and *Mephitis*, where it lies far in towards the *foramen lacerum posticum*. It is relatively closer to the latter orifice in the Skunks than in other genera.

The Internal Structure of the Auditory Bulla.

The bulla of *Meles meles* may be described as representing a common type in the family*.

The tympanic ring projects far into the cavity of the bulla as a large semicircular lamina. The space between it and the roof of the bulla is divided into chambers by a few vertical, arched, bony plates, arising from the lamina and the superjacent roof and extending transversely inwards on to the inner wall. These may be called the rafters. There is also a tolerably large plate rising from the upper side of the tympanic ring in front and extending horizontally forwards to the bottom of the anterior wall of the bulla, terminating internally at a point where the bulla touches the *foramen lacerum medium*. Behind this point the floor of the cavity is subdivided by low anastomosing ridges into a number of pockets.

The posterior portion of the tympanic ring lies just above the *fenestra rotunda* on the periotic bone; and the posterior rafter, rising about one-fourth of the distance from the posterior end of the tympanic ring, arches high above the periotic, and terminates about half-way down the inner wall of the cavity. This rafter, supplemented by the posterior end of the tympanic ring, partially divides the cavity of the bulla into an anterior larger and a posterior smaller chamber. Nevertheless there is a wide passage between them above the periotic bone. The posterior part of the cavity of the bulla is closed behind, and does not extend beyond the limits of the bulla as defined externally.

The bulla of *Martes martes* resembles that of *Meles* in all essential respects, the posterior rafter being well developed; but in *M. foina* all the rafters are less well developed, the posterior being quite short.

In *Charronia flavigula* there is only a single rafter arising from about the middle of the tympanic ring, arching with a strong concave curve to the roof, then descending to the floor along the inner wall of the bulla.

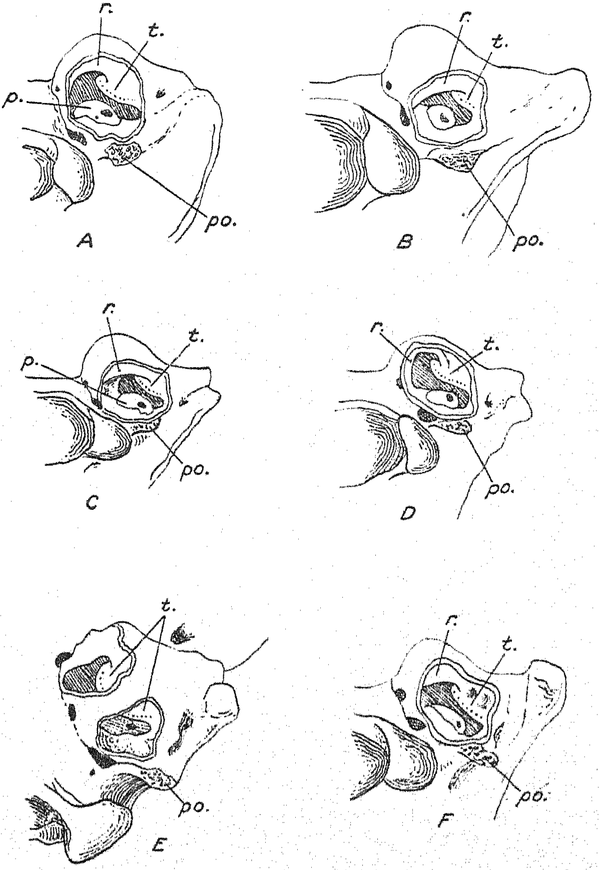
Tayra barbara resembles *Charronia* except that the rafter is less elevated and less arcuate.

Gulo gulo is very like *Meles* and *Martes martes*, but the posterior rafter has the lower edge, not lightly concave as in those forms, but horizontal or inclined slightly downwards towards the inner wall of the cavity. It is thus nearer the periotic bone, and diminishes the height of the passage between the anterior and posterior portions of the bulla.

---

* In this paper the bulla is described as seen when the skull is inverted. Hence the periotic forms part of the floor of its cavity; and the cavity is bounded by the roof above and by the anterior, inner, and posterior walls. Flower described it as seen when the skull is in its natural position, and I followed that course in the case of the Felidæ (Ann. Mag. Nat. Hist. (8) xviii. pp. 326–334, 1916).

Text-figure 16.



A. Bulla of *Tayra barbara* opened from behind.
B. The same of *Gulo gulo*.
C. The same of *Martes martes*.
D. The same of *Martes foina*.
E. The same of *Meles meles* opened from below in front and behind.
F. The same from behind.
Lettering as in Text-fig. 15.

Lutra lutra, *cinerea*, *barang*, and *maculicollis* have a very simple type of bulla, differing from those described above in that the tympanic ring, in conformity with the comparative flatness of the bulla, is almost in contact with the superjacent portion of the roof, to which it is attached by two or three very shallow rafters. The posterior rafter, present in *Meles*, *Gulo*, and *Martes martes*, is undeveloped, the only trace of subdivision of the cavity being supplied by a rafter which extends transversely from the ring along the roof and inner wall of the bulla to a point just behind the orifice of the carotid canal; and, as indicated on the outside of the skull, the cavity of the bulla posteriorly is far in advance of the paroccipital process. Except for its flatness the bulla is very like that of *Tayra* or *Martes foina*.

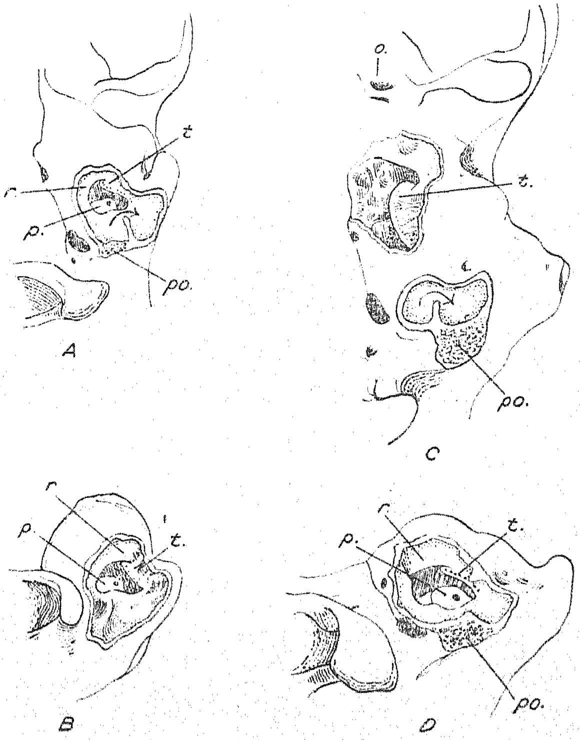
In *Pœcilogale*, judging from a skull with a partially fractured bulla in the British Museum, it seems that the walls of the bulla are thin, not spongy, and that the cavity, reaching posteriorly to the paroccipital, is simple and undivided except by incomplete rafters, and does not communicate with a chamber hollowed out in the mastoid, which is quite small. This genus therefore has a simpler, more primitive bulla than is seen in *Mustela* or in *Ictonyx*.

Another type of bulla is found in *Gale nivalis*, *africana*, *Mustela erminea*, *hibernica*, and *Putorius putorius* and *furo*. The cavity of the bulla is continuous from end to end, being undivided by septa; but it is greatly reduced in size by the thickness of its walls, which, instead of being composed of solid bone, thicker or thinner, as the case may be, in the genera previously described, is composed of spongy bone permeated with air-cells. These fill the entire space above the tympanic ring, and almost obliterate the portion of the cavity behind the petrous portion of the periotic and also the anterior part of the cavity. There is no definite hollow space in the external portion of the periotic; but this bone is spongy and porous like the walls of the bulla itself, and its spaces communicate with the cavity of the bulla.

The bulla of *Helictis* (*H. everettii*) is quite unique. The tympanic ring is fused to the roof but not to the same extent as in *Grisonella* and *Mephitis*, its free edge projecting slightly, even in the middle of its curve, and more so in front and behind. The anterior rafter resembles that of *Grisonella*; but the posterior rafter, rising low down on the tympanic ring behind, runs obliquely forwards and inwards to terminate on the floor of the bulla just inside the point where the orifice of the carotid canal opens. Its inferior edge is closely clamped on to the petrous portion of the periotic except at one point situated externally towards the stylomastoid, where there is a notch in the partition rafter close to the *fenestra rotunda*. Thus the bulla is completely divided into two subequal chambers, except where the notch in question affords a passage between them—a precisely similar formation to that which is well-known in many Æluroidea. The posterior chamber has a few low marginal ridges on its inner and posterior walls, and the anterior end of the anterior chamber has a few ridges in addition to the anterior rafter. The external portion of the periotic is not hollowed.

The bulla of *Mellivora* resembles internally that of *Meles* except that the cavity is posteriorly in communication by means of a tolerably large orifice in the anterior part of the hinder chamber with a smooth-walled cavity hollowed out in the periotic behind the stylomastoid foramen. The posterior rafter is deeper and more arcuate than in *Meles*, and forms a half-partition between the anterior and posterior portions of the cavity of the bulla—and behind it on the inner side a vertical crest of bone juts out from the inner wall of the bulla.

Text-figure 17.



A. Bulla of *Ictonyx* opened from below, the arrow showing the passage between the cavity and the hollow in the external portion of the periotic.
B. The same of *Pœcilictis* opened from behind, showing the extension of the cavity into the occipital and mastoid.
C. The same of *Mellivora* opened from below, the arrow showing the passage between the cavity and the small hollow in the external portion of the periotic.
D. The same opened from behind.

Lettering as in Text-figs. 15 and 16.

Ictonyx is like *Mellivora* except that there is no crest behind the partition on the inner wall of the bulla; and the related genus *Pœcilictis* only differs in the greater size of the supplementary chamber in the periotic and of the space above the tympanic ring.

Taxidea is like *Pœcilictis*. In conformity with the great inflation of the bulla the space between its roof and the tympanic ring is very high and septate. The posterior rafter is continuous with the posterior edge of the tympanic ring, and descends so low that only a small passage is left between its inferior arcuate edge and the periotic. A posterior chamber is thus cut off almost as completely as in some Æluroids. This posterior chamber is extended anteriorly above the tympanic ring on the inner side of the stylomastoid foramen, and it communicates by a wide passage with a large cavity, larger than in *Mellivora*, hollowed out in the periotic between the mastoid and paroccipital processes.

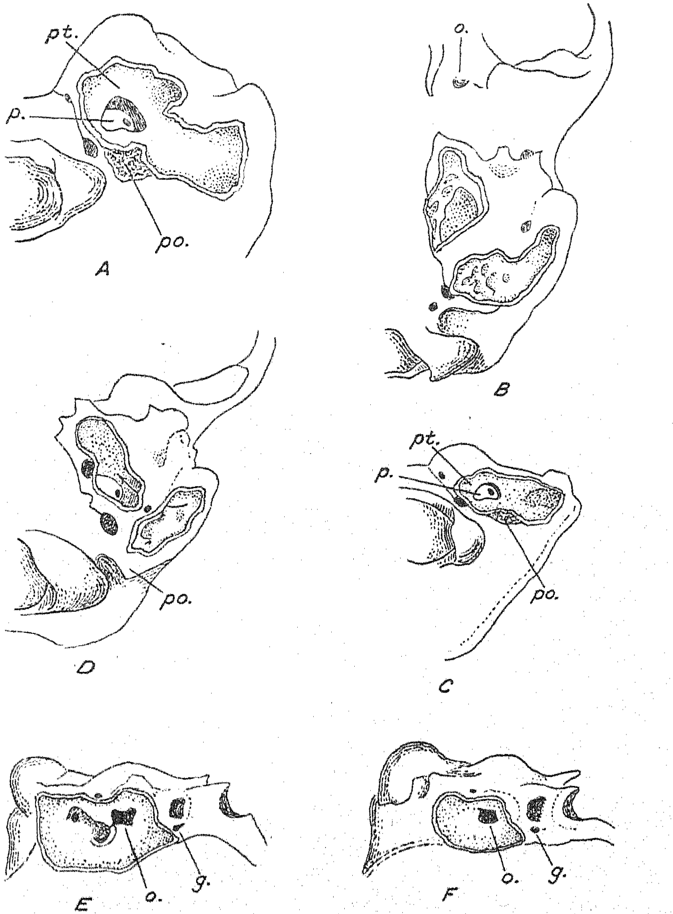
Thus the bulla of *Taxidea* is very different from that of *Meles*, and not essentially like it as Flower stated. It is much more like that of *Mellivora*, although the partition is better developed and the periotic hollow much larger. In *Mellivora*, too, the posterior chamber is not extended forwards above the tympanic ring on the inner side of the stylomastoid.

In *Grisonella* (sp. from Cordova in the Argentine) the roof of the bulla is depressed on to the tympanic ring, and fused with it practically throughout its extent except for the presence of one or two very small cellular spaces in front and behind. The anterior rafter is very large, and rising from the summit of the anterior part of the tympanic ring, descends obliquely downwards and inwards, dividing the anterior part of the cavity, which is further broken up by anastomosing ridges, into an upper and a lower portion. Just behind the posterior end of the ring but confluent with it arises a comparatively large arched rafter which, crossing the roof, descends along the inner wall of the bulla, dividing the cavity into an anterior and posterior chamber which communicate by a comparatively narrow passage above the periotic. The posterior chamber has septa on the inner wall and anastomosing ridges on the floor, and anteriorly just behind the main transverse septum formed by the posterior rafter there is a passage by which the posterior chamber opens into the hollowed external portion of the periotic. The floor of this hollow is uneven with ridges and shallow pits.

It is interesting to note that the bulla of *Grisonella* is widely different from that of *Tayra*, although the two genera were formerly regarded as identical. In possessing a hollowed periotic chamber communicating with the cavity of the bulla, *Grisonella* resembles *Mellivora*, *Ictonyx*, and *Taxidea*, and is further like the latter in the origin of the posterior rafter from the posterior end of the tympanic ring. But in none of these genera is the ring confluent with the roof of the bulla as it is in *Grisonella*.

A skull of *Lyncodon*, with a broken bulla, in the British

Text-figure 18.



A. Bulla of *Taxidea* opened from behind, showing the nearly complete partition between the posterior and anterior chambers, and the extension of the posterior into the external portion of the periotic.

B. The same of *Grisonella* sp. opened from below, showing the extension of the posterior chamber into the external portion of the periotic.

C. The same opened from behind, showing the complete partition and the extension of the posterior chamber into the external portion of the periotic.

D. Bulla of *Mephitis* opened from below showing the absence of partition, the arrow indicating the passage from the cavity into the hollow of the external portion of the periotic.

E. Hollow in external portion of periotic of *Mephitis* opened from the outside.

F. The same of *Conepatus*.

Lettering as in Text-fig. 15, with the addition of *o*, the orifice by which the cavity of the bulla opens into the periotic hollow.

Museum shows that the cavity is broken up by trabeculæ into spaces which extend into the mastoid. It is not possible, however, to ascertain from this specimen whether the cavity, before fracture, was divided by a partition into two chambers as in *Grisonella* or not.

In *Mephitis*, *Spilogale*, and *Conepatus* the bulla is still more peculiar. As in *Grisonella*, the tympanic ring is fused with the roof of the bulla and the cavity of the latter is a hollow space, with at most a few septa or bony ridges, which is closed just behind the periotic by a thickish wall of bone lying between the stylomastoid foramen and the *foramen lacerum posticum*; but opposite the outer side of the periotic there is a tolerably large oval orifice by which the cavity of the bulla communicates with a large hollow space occupying the expanded area of the skull between the auditory orifice and a point on the occipital crest above the paroccipital process. Behind the bulla externally there is a tolerably long, flat area running back to the paroccipital process, which, as in *Lutra*, is placed some distance behind the bulla.

In *Mephitis* and *Spilogale* the cavity in the periotic runs inwards by means of a narrow passage up to the *foramen lacerum posticum*, and the posterior margin of the orifice, by which the cavity communicates with the bulla, is produced into a crescentically curved ridge of bone. This ridge and the narrow passage running to the *foramen lacerum posticum* are absent in *Conepatus proteus*, the walls of the cavity being undifferentiated.

In the British Museum there is a skull of *Mydaus* with a broken bulla, which seems to show that in essential points the bulla of this genus resembles that of *Mephitis*. The cavity of the bulla, for instance, comes to an end posteriorly just behind the petrous portion of the periotic, and on the outer side of this bone there is an orifice by means of which the cavity of the bulla communicates with the hollowed mastoid portion of the periotic.

The following table summarises the principal variations in the structure of the bulla:—

a. Cavity of bulla closed behind, not communicating with a hollow space in the external portion of the periotic, the latter being solid or merely permeated with air-cells.
  b. Bulla distinctly divided into two subequal chambers by a bony partition running obliquely inwards and forwards from posterior end of tympanic ring to carotid foramen, the two chambers communicating by means of a notch in the lower edge of the partition behind posterior end of petrous portion of periotic .... *Helictis.*
  b′. At most an incomplete partition passing transversely from posterior portion of tympanic ring to the *foramen lacerum posticum.*
    c. Walls of bulla exceedingly thick, permeated everywhere with air-cells. No partition .... *Mustela, Putorius,* [*Vormela*].
    c′. Walls of bulla thin, without noticeable air-cells.
      d. Tympanic ring closely applied to roof of bulla, the posterior end of which is far in advance of the paroccipital. *Lutra.*

- *d'*. Tympanic ring projecting as a strong semicircular ridge into cavity of bulla and attached to its roof by septa which, rafter-like, pass inwards and downwards along roof and inner wall of the cavity.
  - *e*. Cavity very incompletely divided by a median rafter arching high above the tympanic ring, leaving a wide space between its inferior edge and petrous portion of periotic .... *Martes foina*; *Charronia*; *Tayra*.
  - *e'*. Cavity much more completely divided by an additional rafter, the inferior edge of which extends nearly horizontally inwards and approaches much nearer the petrous portion of the periotic .... *Martes martes*; *Gulo*; *Meles*.
- *a'*. Cavity of bulla opening behind into a larger or smaller hollow space in external part of periotic.
  - *f*. Cavity undivided, communicating with periotic hollow by means of a well-defined orifice opposite outer side of petrous portion of periotic (tympanic ring fused with roof of bulla).
    - *g*. Walls of periotic hollow undifferentiated .... *Conepatus*.
    - *g'*. Walls of periotic hollow with crescentic ridge and a passage reaching inwards to *foramen lacerum posticum* ...... *Mephitis*, *Spilogale*.
  - *f'*. Cavity more or less divided by rafter-like partition into an anterior and a posterior chamber, the latter opening into hollow of periotic.
    - *h*. Tympanic ring fused with roof of bulla; a very narrow space, nearly filled by the periotic between the two chambers; the chambers much broken up by trabeculæ... *Grisonella*.
    - *h'*. Tympanic ring projecting into bulla, the structure of which closely resembles that described under heading *d'*.
      - *i*. Periotic hollow smaller, only reaching to a point halfway between paroccipital and tip of mastoid .... *Mellivora*.
      - *i'*. Periotic hollow larger, extending to tip of hollow mastoid.
        - *k*. A bony septum separating posterior chambers of the bulla from periotic hollow behind and leaving a comparatively narrow passage of communication in front; inferior edge of partition between chambers of bullæ evenly concave .... *Ictonyx*.
        - *k'*. Posterior chamber of bulla and periotic hollow confluent throughout their extent; inferior edge of partition between chambers angularly arcuate over petrous.
          - *l*. Bulla abutting behind against nearly obsolete paroccipital and confluent in front with hamular process of pterygoid, as in *Ictonyx* .... *Pœcilictis*.
          - *l'*. Bulla not reaching the stout, projecting paroccipital, and ceasing in front far behind hamular ... *Taxidea*.

The three genera *Pœcilogale*, *Lyncodon*, and *Mydaus* have been omitted from the table because from want of material my examination of the bullæ was imperfect. So far, however, as the available evidence goes they would fall provisionally as follows:—*Pœcilogale* under *d* alongside *Lutra* because the roof of the bulla is thin and close to the tympanic ring, and its cavity is undivided and not in communication with a hollow in the periotic. The shape of the bulla is, however, very different from that of *Lutra*. It is long, abuts against the paroccipital behind, and has a short auditory tube as in *Mustela*. Its likeness to the bulla of *Lutra* is no evidence of affinity between the two genera.

It merely means, in my opinion, that they have inherited bullæ of a primitive kind, derivable from the *Martes-Tayra* type, the flattening in the two cases having been independently acquired. *Lyncodon* must be provisionally placed alongside *Grisonella*, and *Mydaus* with *Mephitis*, *Spilogale*, and *Conepatus*.

Since such otherwise dissimilar genera as *Meles* and *Gulo* or *Martes* have similar bullæ, it is probable that that type of bulla is the most primitive in the Mustelidæ. The rest of the bullæ may be derived from it by modifications in different directions. The flattening down of the roof on to the tympanic ring and the shortening of the posterior portion of the cavity gave rise to the bulla of *Lutra*; similar flattening of the roof and the development of a complete oblique partition to that of *Helictis*; thickening of the walls with spongy bone filling the spaces between the main septa to that of *Mustela*; and the opening of the posterior chamber into the hollow of the periotic to that of *Mellivora*. From the latter may be derived the bullæ of *Ictonyx*, *Pœcilictis*, and *Taxidea* by extension of the periotic space, and in the case of *Grisonella* this was accompanied by the flattening of the bulla and the confluence of its roof with the tympanic ring and reduction of the posterior chamber. The bulla of *Mephitis* and other Skunks may also be derived from the type seen in *Mellivora* by the disappearance of the partition behind the petrous portion of the periotic, shortening of the portion of the cavity behind it, and the forward movement of the orifice by which the cavity communicates with the greatly enlarged periotic hollow.

25. On the Venous System of the Lizard *Varanus bengalensis* (Daud.).

By Gobind Singh Thapar, M.Sc., Professor of Zoology, Canning College, Lucknow*.

[Received April 5, 1921 : Read May 10, 1921.]

(Text-figures 1–4.)

The only data we possess concerning the venous system of the genus *Varanus* appear to be contained in the work of Corti, 'De Systemate Vasorum Psammosauri grisei,' 1847 (which I have not seen; the observations are reproduced in Bronn's Thierreich, vol. vi. Abt. iii. Reptilien, by C. K. Hoffmann, p. 1010); Hochstetter, "Beiträge zur Entwickelungsgeschichte des Venensystems der Amnioten, II. Reptilien (*Lacerta*, *Tropidonotus*)," Morph. Jahrb. xix. 1893, p. 464 (mainly the renal and hepatic portal systems of *V. arenarius*, according to Beddard a synonym of *V. griseus*); Beddard, "On the Venous System in certain Lizards," P. Z. S. 1905, i. p. 447 (*V. griseus*), and Beddard, "On the Vascular System of *Heloderma*, with Notes on that of the Monitors and Crocodiles," P. Z. S. 1906, ii. p. 610 (*V. griseus*, *niloticus*, and *exanthematicus*).

These descriptions, however, do not completely apply to the present species, *V. bengalensis*, common in and near Lucknow, and it seems desirable, therefore, to record the results of my investigation.

Besides ordinary dissections, injections were made through the anterior abdominal vein, using a thick solution of gum arabic to which a little colouring matter—carmine or methyl blue—was added. The fluid passes completely into the system, and it is easy then to dissect out even the finer vessels. I have used this fluid in preference to gelatine, as it can be employed cold, and sets satisfactorily after being placed for a short time in alcohol, swelling the vessels. I have to thank Prof. H. C. Ahuja, of the Central Hindu College, Benares, for supplying me with the necessary literature; and my grateful acknowledgments are due to my friend Mr. S. K. Zibbu, of the Lucknow Christian College, for the assistance he has given me in the course of my work.

I. The System of the *Anterior Vena Cava* (text-fig. 1).

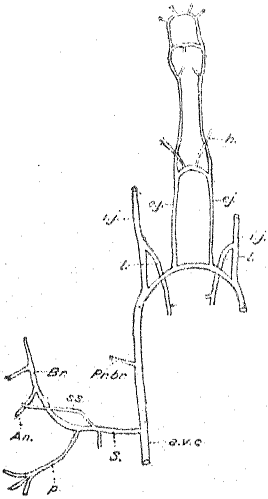
(1) The *External Jugular Vein* (*e.j.*). It is stated that this vein is ordinarily absent on the left side in Lacertilia; in the present species, however, it occurs on both sides, the vessels running parallel on each side of the trachea. It joins the internal jugular at the base of the neck. The external jugulars communicate with each other by four transverse connections, the plexuses. The first plexus is situated at the level of the thyroid gland, close to the place of union of the external with the internal

---

* Communicated by Dr. J. Stephenson, F.Z.S.

jugular vein. The second plexus occurs a little higher up, near the hyoid, from which it receives branches (*h.*). The third and fourth plexuses are near each other, on the floor of the buccal cavity. The formation of plexuses between the external jugular veins is essentially an avian character, and I am not aware that it has hitherto been described in any Lacertilian.

Text-figure 1.



The Anterior Vena Cava and its branches.

a.v.c., anterior vena cava; *an.*, antebrachial; *br.*, brachial; *e.j.*, external jugular; *h.*, hyoidean; *i.j.*, internal jugular; *l.*, lateral vein; *p.*, pectoral; *pr.br.*, prebrachial; *s.*, subclavian; *ss.*, subscapular.

(2) The *Internal Jugular Vein* (*i.j.*) receives a short vessel, the lateral vein (*l.*), from the hinder region of the neck.

(3) The *Prebrachial* (*pr.br.*) joins the vena cava at the junction of the neck with the body. It is a vessel of fair size, running along the preaxial border of the arm.

(4) The *Subclavian Vein* (*s.*) is a very large vessel running along the postaxial side of the arm; it receives many branches from the arm, shoulder, and chest, the chief of which are

(*a*) Subscapular (*ss.*), from the muscles of the back,
(*b*) Pectoral (*p.*), from the pectoral muscles,
(*c*) Brachial (*br.*), from the arm and hand,
(*d*) Antebrachial (*an.*), from the forearm.

(5) The *Azygos Vein* (text-fig. 3, *az.*), which enters the right anterior vena cava, is a fairly large vessel formed by the union of two branches, a vertebral (*v.*) from the vertebral column, and a parietal (*pa.*) from the body-wall. Beddard states that in *V. griseus* the parietal branch of the azygos is connected with

the suprarenal portal; there is, however, no such connection in *V. bengalensis*. The *lateral parietal vein* (*l.pa.*), running laterally along the body-wall, communicates with it; behind, this vein forms an anastomosis with the dorsal parieto-hepatic vein. The vertebral branch of the azygos disappears from view at the side of the vertebral column.

II. The *Posterior Vena Cava* (text-fig. 4).—This vessel begins at the hinder end of the body a little behind the kidneys, and bifurcates into two branches, each of which runs in a groove along the ventral surface of the kidney. Leaving the kidneys ("posterior cardinals," Beddard) they traverse the suprarenal bodies, beyond which they again unite. The vessel passes through the appendage of the right lobe of the liver and discharges into the sinus venosus. The anatomy thus indicates the origin of the posterior vena cava from two originally distinct vessels, the fusion of which to form a single trunk is here still incomplete.

III. The *Hepatic Portal System* (text-fig. 2) is peculiar in the present species. The *femoral vein* (*f.*) is formed by the union of several small vessels from the muscles of the leg and the pelvis; on entering the trunk it divides into two branches, the pelvic, and one which I propose to call the ischio-mesenteric. The *pelvic vein* (*p.*) runs forward along the inner border of the corpus adiposum of its side, and after receiving the sciatic (*sc.*) from the posterior region of the leg and a varying number (4–5) of veins from the fat-bodies (f_1–f_4), unites with its fellow of the other side to form a median abdominal vein; the pelvic vein also receives two or three dorso-lumbar veins from the body-wall.

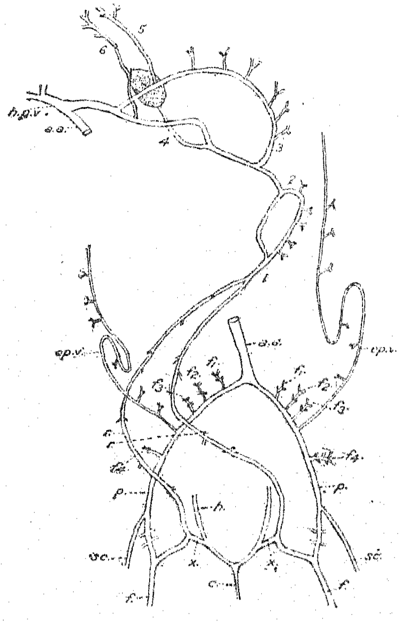
The *epigastric veins* (*ep.v.*) are two in number, and are described by Beddard as originating in *V. griseus* from the sciatic veins. In the present species I find that they arise from the pelvic; each is a fairly long narrow vessel running dorsally over the fat-body, from which it receives a few branches. It then curves backwards, and again forwards, assuming a position ventral to the fat-body, and, receiving many branches from the parietes, proceeds forwards to open into the corresponding lobe of the liver at its anterior ventral margin. Before entering the liver each is joined by a ventral parieto-hepatic vein from the ventral body-wall.

The *anterior abdominal ventral vein* (*a.a.*), formed by the union of the pelvic veins, is a single vessel throughout its course, and joins the hepatic portal vein.

The other branch of the femoral, which I have called the *ischio-mesenteric* (*r.*), is an altogether new vessel, not so far described by any observer. It receives a small offshoot (*x.*) from the hypogastric, and runs along the rectum, receiving minor branches from the rectum and cæcum. In front of the cæcum the two ischio-mesenterics unite to form one of the main roots of the hepatic portal vein.

The *hepatic portal vein* (*h.p.v.*) forms two complete loops in the mesentery of the small intestine (text-fig. 2); in the course of the second loop it receives splenic, pancreatic, and gastric veins. It runs forwards to the hinder end of the median sulcus of the liver, and after receiving the anterior abdominal vein divides into two branches, one entering each lobe of the liver towards its dorsal side.

Text-figure 2.



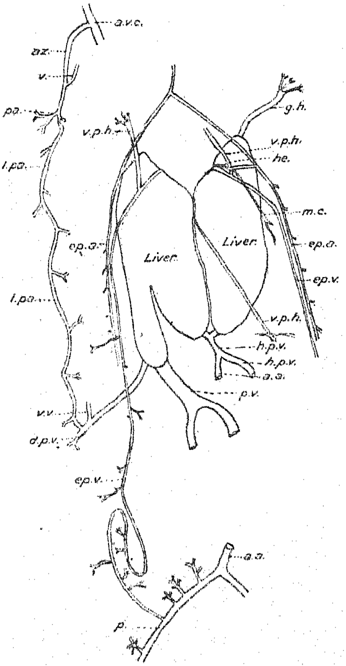
The Hepatic Portal Vein and its connections.

aa., anterior abdominal vein; *c.*, caudal; *ep.v.*, epigastric; *f.*, femoral; f_1-f_4, veins from the fat-body; *h.*, hypogastric; *h.p.v.*, hepatic portal vein; *p.*, pelvic; *sc.*, sciatic; *r.*, ischiomesenteric; 1, 2, 3, 4, 5, veins forming the hepatic portal; 6, gastric; *x.*, connection between hypogastric and ischiomesenteric veins.

It would thus appear that all the blood from the limbs and alimentary canal passes through the liver before entering the posterior vena cava. A large part of the blood from the hinder region passes along the ischio-mesenteric vein into the liver, while a small part enters the kidneys by way of the hypogastric veins. Thus while the hepatic portal system is increasing in complexity the renal portal is reduced. The short connection between the hypogastric and ischio-mesenteric veins would allow the blood to flow from the ischio-mesenteric to the hypogastric or *vice versa*; but the possibility of a flow into the hypogastric is perhaps diminished by reason of the direction of the connecting vessel, taken in conjunction with the forward stream into the hypogastric from the tail.

The *dorsal parieto-hepatic vein* (*d.p.v.*, text-fig. 3). The right lobe of the liver has a small elongated appendage on the dorsal side towards its hinder end, which encloses in its whole length the posterior vena cava. Into this appendage opens a vessel from the dorsal body-wall, the dorsal parieto-hepatic vein, supported by a pocket-shaped fold of peritoneum which, as in *Iguana* and *Heloderma*, attaches the appendage to the body-wall. This vein is described by Hochstetter, and by Beddard, who finds it in other species of *Varanus*, in the same position. The dorsal parieto-hepatic is formed by the union of the dorso-lateral vein from the body-wall with a vertebral vein from the vertebral column; the dorso-lateral forms an anastomosis with the parietal vein, as previously stated.

Text-figure 3.



The Veins in connection with the Liver.

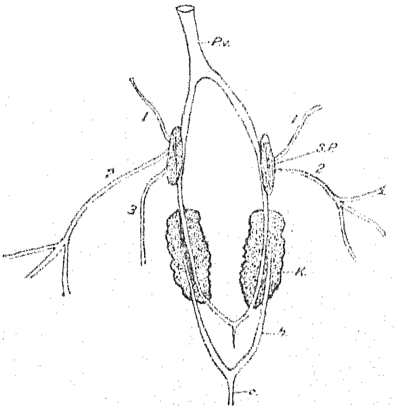
d.p.v., dorsal parieto-hepatic vein; *ep.*, epigastric; *g.h.*, gastro-hepatic; *h.*, hepatic vein; *p.v.*, posterior vena cava; *v.p.h.*, ventral parietohepatic veins.

Another vessel opens into the left lobe of the liver at its extreme anterior tip—the *gastro-hepatic* (*g.h.*), coming directly from the stomach. Hochstetter noted its position in *V. griseus*, and Beddard in *V. niloticus* and *exanthematicus*. I find exactly the same state of affairs in *V. bengalensis*.

The *ventral parieto-hepatic veins* (*v.p.h.*) are three in number. Two of these are laterally situated, and are connected with the corresponding epigastric vein close to its entrance into the liver. The third is a median vessel from the hinder end of the body, which receives smaller branches from the sides and enters the liver at the median sulcus near its anterior end.

IV. The *Suprarenal Veins* (text-fig. 4, 1, 2, 3).—The suprarenal bodies are situated in front of the kidneys, and each encloses the corresponding branch of the posterior vena cava. Each has its own blood-supply; the right suprarenal portal system consists of three veins: one formed by the union of three vessels of the lateral body-wall; the second, from the body-wall near the vertebral column; and the third, from the omentum. The left suprarenal portal is formed by two veins only, the vein which on the right side runs close to the vertebral column being absent.

Text-figure 4.



The Posterior Vena Cava and its connections.

c., caudal vein; *h.*, hypogastric; *k.*, kidneys; *p.v.*, posterior vena cava; *s.p.*, suprarenal body; 1, 2, 3, veins forming the suprarenal portal system.

The chief peculiarities of the venous system of *Varanus bengalensis* are thus:—

(1) The presence of jugular plexuses like those of birds, formed by the external jugulars.

(2) The azygos vein joins the right anterior vena cava, and one of its branches forms an anastomosis with the dorsal parieto-hepatic veins.

(3) Presence of an ischio-mesenteric vein, and consequent complication of the hepatic portal system.

(4) The origin of the epigastric veins from the pelvic and not from the sciatic.

26. Abnormalities in the Common Frog (*Rana temporaria*).

By J. H. LLOYD, M.Sc., F.Z.S., Zoological Department, University College, Cardiff.

(Text-figure 1.)

[Received January 13, 1921: Read April 5, 1921.]

Both specimens described in the following notes were discovered on dissecting a number of frogs for class purposes at the beginning of the present session.

SPECIMEN A. *Persistence of the right Posterior Cardinal vein in an adult male* Rana temporaria.

The occasional persistence of the posterior cardinal vein was first noted by Howes (2) in 1888, in an adult female *Rana temporaria*. In this specimen the postcaval vein was normally developed and the persistent left posterior cardinal functioned as an azygos vein. The cardinal was continuous posteriorly with the renal portal vein. According to Parker (6), Howes afterwards came across another frog in which an almost similar arrangement occurred.

In the following year Parker (6) described a male frog with a persistent left posterior cardinal vein, in which the hepatic veins opened direct into the sinus venosus.

In 1905 Woodland (7) described a male *Rana temporaria* in which a large posterior cardinal vein persisted which was continuous posteriorly with the enlarged right renal portal vein. The venous blood was supplied to both kidneys by the left renal portal only.

O'Donoghue (4 & 5) has described eight cases of the persistence of posterior cardinal veins in adult frogs. Seven of his specimens were males (six *Rana temporaria* and one *Limnodynastes peronii*), and the other was a female *Rana temporaria*. The majority of his specimens in addition exhibited abnormalities of the renal portal veins.

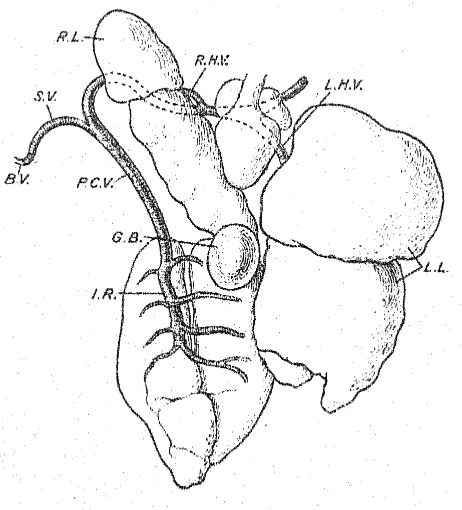
Description of Specimen A.

This specimen exhibits a persistent right posterior cardinal vein which runs from the anterior of the interrenal portion of the postcaval vein, and opens anteriorly into the subclavian vein about halfway along its length. The interrenal vein is normally developed and receives the renal and spermatic veins from the kidneys and spermaries of right and left sides. There is absolutely no trace of the left posterior cardinal vein or of the postcaval vein anterior to the kidneys. The renal portal veins exhibit no abnormalities.

The liver in this specimen is also peculiar. The left lobe is normally developed and the left hepatic vein opens directly into the sinus venosus. The right lobe is an elongated, slightly dorso-ventrally flattened, cylindrical structure which is anteriorly directed and terminates near the posterior edge of the mylohyoid muscle. This lobe is divided into two portions by a transverse constriction. About halfway along its length on the mesial side of the dorsal surface, a hepatic vein runs out and opens into the right precaval vein. The internal and external jugular veins enter the precaval together dorsal to the abnormal lobe of the liver.

As far as I can ascertain this is the only case yet recorded of a hepatic vein opening into a precaval. This irregularity is obviously due to the abnormal condition of the liver.

Text-figure 1.



Sketch of specimen A from ventral surface, shewing persistent right posterior cardinal vein and abnormal liver. B.V. brachial vein; G.B. gall-bladder; I.R. interrenal vein; L.H.V. left hepatic vein; L.L. left lobe of liver; P.C.V. right posterior cardinal vein; R.H.V. right hepatic vein; R.L. right lobe of liver; S.V. subclavian vein.

According to Hochstetter (**1**) the posterior portions of both posterior cardinal veins fuse in Amphibia to form the interrenal ("*Urniere abschnitte*") portion of the postcaval, the anterior portion ("*Leberabschnitt*") of the latter being formed by a venous connection between the anterior end of the interrenal vein and the tip of the liver. It is suggested that in the specimen described above the formation of this venous connection was interferred with by the growth of the liver towards the anterior end of the animal. (Kerr (3) has pointed out "that in *Lepidosiren* and *Protopterus*, the tip of the liver is in contact, and fused, with the tip of the right kidney.") This necessitated the persistence of one of the posterior cardinal veins to carry on the functions of the postcaval in returning blood from the posterior end of the body.

It is interesting to note that this specimen being a male supports O'Donoghue's (4) suggestion that the absence of the postcaval and persistence of a posterior cardinal vein appears to be correlated with the sex of the animal.

SPECIMEN B. *Abnormal Genital Organs in a male* Rana temporaria.

This specimen possessed a greatly hypertrophied testis, which completely covered the left kidney, when viewed from the ventral surface. There was absolutely no trace of a testis on the right side, but the fat-body on both sides was well developed, that on the right side being attached to the kidney.

The right kidney was about one-eighth of an inch shorter than the left, and was distorted in such a way as to give it a cylindrical appearance, and to cause the ureter to run on the dorsal surface instead of on the outer edge. Both kidneys were so closely apposed that it was difficult to ascertain whether there was any actual fusion. There was a well developed seminal vesicle attached to each ureter, and from the fact that both seminal vesicles were apparently filled with sperms it seems probable that there was some degree of fusion.

The left renal portal vein was normal but the right renal portal was much reduced in size.

LITERATURE.

1. HOCHSTETTER, F.—Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische. Morphol. Jahrb. Bd. 13, 1888.
2. HOWES, G. B.—Note on the Azygos Vein in the Anurous Amphibia. Proc. Zool. Soc. 1888, p. 122.
3. KERR, J. GRAHAM.—Note on the Posterior Vena Cava in *Polypterus*. Proc. Roy. Physiol. Soc. Edinburgh, vol. xviii. 1910.
4. O'DONOGHUE, C. H.—The Persistence of Posterior Cardinal Veins in the Frog, together with some Remarks on the Significance of the Renal Portal System. Anat. Anz. Bd. 36, 1910.
5. O'DONOGHUE, C. H.—Further Instance of the Persistence of Posterior Cardinal Veins in the Frog. Anat. Anz. Bd. 43, 1913.

6. PARKER, W. N.—On the Occasional Persistence of the left Posterior Cardinal Vein in the Frog, with Remarks on the Homologies of the Veins in the Dipnoi. Proc. Zool. Soc. 1889, p. 145.
7. WOODLAND, W.—On a New Mode of Persistence of the Posterior Cardinal Vein in the Frog: with a Suggestion as to the Phylogenetic Origin of the Post-caval Vein. Zool. Anz. vol. xxviii. 1905.

27. The Comparative Anatomy of the Tongues of the Mammalia.—IV. Families 3 and 4. Cebidæ and Hapalidæ. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received April 15, 1921: Read May 24, 1921.]

(Text-figures 37–52.)*

CONTENTS.

	Page
Introduction	497
Family Cebidæ	497
Pigmentation	497
Genus *Cebus*	498
Genus *Ateles*	502
Genus *Lagothrix*	506
Genus *Saimiris*	509
Genus *Callicebus*	509
Genus *Aotus*	511
Genus *Pithecia*	512
Genus *Cacajao*	514
Genus *Alouatta*	515
Summary	516
Family Hapalidæ	517
Genus *Hapale*	520
Genus *Leontocebus*	520
Genus *Mystax*	523
Genus *Œdipomidas*	523
Summary	523
Bibliography	524

INTRODUCTION.

The literature of the Cebidæ and Hapalidæ contains several papers on the tongues of *Cebus*, *Ateles*, and *Callithrix* (=*Hapale*), but few on those of other genera. The objects of this paper, which is based on fifty-five specimens, are to supplement existing accounts, and describe several tongues for the first time.

The tongues of the Cebidæ and Hapalidæ resemble those of the Cercopithecidæ in the characters of the apex and lateral borders; and they agree with them in that the foramen cæcum, lytta, plicæ fimbriatæ, and apical gland of Nuhn or Blandin are absent.

I have given the measurements of fresh specimens only, for a list of the dimensions of preserved ones is worthless.

I have employed Pocock's nomenclature (**12**) for the Hapalidæ.

Family CEBIDÆ.

Pigmentation.—Many of the tongues of the Cebidæ are pigmented, and the colour is evenly distributed over the entire dorsum, or arranged in a definite pattern; on the inferior surface it covers the parts around the frenal lamella which, as a rule, is colourless. The vallate and fungiform papillæ may be colourless or pigmented.

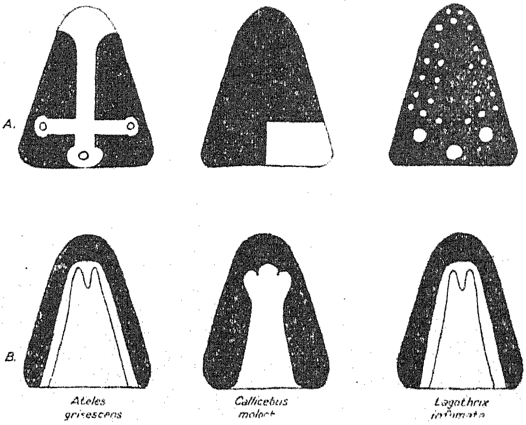
If several specimens of each pigmented species are examined it will be seen how the distribution of the pigment varies greatly, so the colour is of no value for purposes of classification.

---

* The explanation of the lettering of the Text-figures is given in the text.

Several forms of pigmentation are shown diagrammatically in text-fig. 37, but the descriptions are given with each species.

Text-figure 37.



Patterns of pigmentation of the tongue: A. dorsum; B. inferior surface.

Genus Cebus.

The Brown Capuchin (*C. fatuellus*).

The largest of three specimens exhibited the following *measurements*:—total length 5·45 cm.; length of the oral part 3·9 cm.; length of the pharyngeal part 1·55 cm.; width between the lingual attachments of the palato-glossal folds 2·1 cm.

The Circumvallate Papillæ.—Specimen No. 1 (text-fig. 38 A, E, & F).—Three papillæ form an isosceles triangle with the apex behind. Each lies in the centre of a low, flat, circular elevation which is crowded with small cylindrical conical papillæ. Only a small part of each papilla projects beyond the vallum. The basal papilla is level with the laminæ of the posterior half of its corresponding lateral organ. Specimen No. 2 (text-fig. 39 A).—Five vallate papillæ form a V. The anterior papillæ are circular and large, the posterior papilla is large and oval, and the mesial papillæ are small and circular. All are recessed within their well-marked fossæ.

The Fungiform Papillæ (text-fig. 38 A, B, & H).—The papillæ, which have a pearly appearance, form a dorsal bounding zone on which they have the usual arrangement in rows and clusters, but the transverse rows extend far forwards at the expense of the apical cluster. On the inferior surface there are two rows—an inner one of closely-set large papillæ, and an outer row of small discrete ones (text-fig. 38 B, *b*).

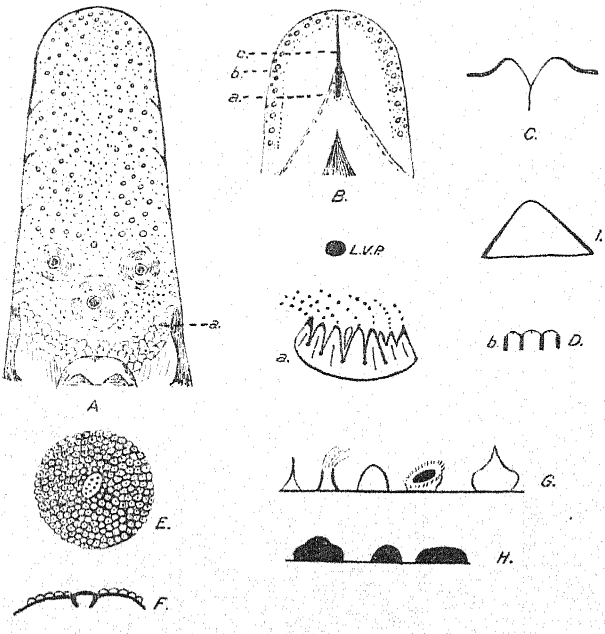
They are hemispherical, flat, or provided with a central elevation, and none are overlapped by conical papillæ.

The Conical Papillæ (text-fig. 38 A, B, & G).—Although they have the usual distribution according to size, and their points run in the usual directions, they are irregular in arrangement on the oral part of the dorsum. They are disposed in oblique chains on the base of the tongue. This lack of definite arrangement in clusters and rows on the oral part of the dorsum is very common on the tongues of the Cebidæ, and rare in the Cercopithecidæ. On the lateral borders and inferior surface they are very closely aggregated, but have no definite arrangement.

They are filiform or cylindrical, and have one or more points.

Lymphoid Tissue and Glands (text-fig. 38 A, *a*).—The base of the tongue is covered with nodules, or is delimited by a crescentic zone of elevations. A few orifices of ducts and pits are present.

Text-figure 38.



The tongue of *Cebus fatuellus*.

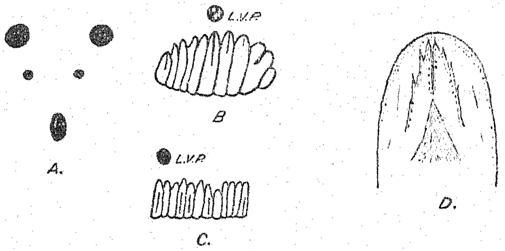
The Lateral Organs (text-figs. 38 D and 39 B & C).—The appearances vary greatly in different examples. They may form concave bodies on the sides and dorsum (text-fig. 38 D), convex bodies on the sides and dorsum (text-fig. 39 B), or long rows of laminæ and sulci on the inferior surface (text-fig. 39 C); the concavities or convexities face the lateral vallate papillæ (L.V.P.). The laminæ are rounded or pointed, and many are traversed by secondary sulci. In two specimens the following measurements, etc., were observed:—

	Length.	*Laminæ.*	*Sulci.*
Specimen No. 1.			
Right organ	1·1 cm.	9	10
Left organ.........	·9 cm.	10	11
Specimen No. 2.			
Right organ	1·1 cm.	9	10
Left organ.........	·8 cm.	12	13

The Frenal Lamella (text-figs. 38 B, *a*, and 39 D).—The triangular lamella has a bifid apex, and the edges, which extend postero-laterally as far as the middle of the lateral organs, may be plain or have long sharp processes. The free part, which is triangular on section (text-fig. 38 I), has a ridge on its upper surface.

The Ventral Papillary Border (text-fig. 38 B, *b*) is narrow, and the arrangement of its conical and fungiform papillæ has already been described.

Text-figure 39.



The tongue of *Cebus fatuellus.*

The Ventral Mesial Sulcus (text-fig. 38 B, *c* and C) is narrow and deep anterior to the frenal lamella (text-fig. 38 A, *c*). Posteriorly it is wide and triangular (text-fig. 38 C) and lodges the ridge on the upper surface of the lamella.

The *frenum* is short and thick. It passes along with the lamella into the wide part of the ventral median sulcus.

The White-fronted Capuchin (*C. albifrons*).

The following *measurements* refer to the larger of two specimens:—total length 3·6 cm.; length of the oral part 3·1 cm.; length of the pharyngeal part ·5 cm.; width between the lingual attachments of the palato-glossal folds 1·6 cm.

The Circumvallate Papillæ (text-fig. 40 A).—Three papillæ form a triangle, but none are situated on elevations as in *C. fatuellus.* The basal papillæ are circular, glistening, and slightly retracted, but the apical papilla is deeply recessed (*a*). The fossæ are all well-marked and the vallums are nodulated. The right basal papilla (*b*) is compound, but all the others are simple (*c*). The vallate area is crowded with conical papillæ, and a fungiform papilla bisects the base.

The *Fungiform Papillæ* have a similar arrangement to those of *C. fatuellus*, and exhibit the same characters.

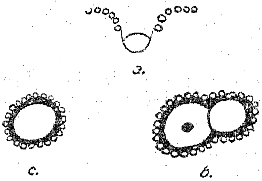
The Conical Papillæ have no definite arrangement in clusters and rows, but they increase in size in the usual manner. None overlap the vallate and fungiform papillæ.

Lymphoid Tissue and Glands.—The base of the tongue is covered with nodules, but no duct orifices are visible through the lens. They are intermingled with conical papillæ.

The Lateral Organs lie on the dorsum and lateral borders of the tongue, and are curved with the convexities forwards. Their surfaces are smooth, and some are traversed by secondary sulci. The inner ends of the laminæ are pointed. Both organs have nine laminæ and ten sulci.

The Inferior Surface.—The *ventral papillary border* is narrow round the apex, and widens on the edges of the inferior surface. Its fungiform papillæ are arranged in two rows as in *C. fatuellus*. The *ventral mesial sulcus* is short, narrow, and deep. It opens posteriorly into a triangular fossa, which also receives the frenum. The *frenal lamella* is triangular, with a bifid apex and serrated edges which extend postero-laterally as far as the middle of the lateral organs.

Text-figure 40.



The vallate papillæ of *Cebus albifrons*.

The Weeper Capuchin (*C. capucinus*).

Several authors have described the tongue of *C. capucinus*, and the following arrangements of the vallate papillæ have been recorded:—

(1) Three papillæ in a triangle....................	Mayer (**4**).
(2) Four papillæ as a double-pair	Mayer (**4**).
(3) Three papillæ in a triangle	Flower (**3**).
(4) Three papillæ in a triangle (in 5 cases) ...	Münch (**5**).

The White-throated Capuchin (*C. hypoleucos*).

Tuckerman (**9**) described the macroscopic and microscopic appearances, and recorded three papillæ in the form of a triangle.

The Horned Capuchin (*C. apella*).

F. J. C. Mayer (**4**) pointed out that the tongue has four vallate papillæ, and nine sulci in the lateral organs.

Podwisotsky (**7**) described six papillæ arranged in the form of a **V**. He also described the lingual glands which are well-developed.

Boulart and Pilliet (**10**), Cuvier (**2**), and Münch (**5**) state that the triangular pattern is the usual arrangement of the vallate papillæ in the genus *Cebus*. It is present in the majority of my specimens, but the **V**-arrangement and double-pair type appear in the remainder.

Genus Ateles.

The Grizzled Spider Monkey (*A. grisescens*).

Measurements:—total length 3·6 cm.; length of the oral part 2·5 cm.; length of the pharyngeal part 1·1 cm.; width between the lingual attachments of the palato-glossal folds 1·7 cm.

Pigmentation.—The apex and a small area of the dorsum behind it are unpigmented. Behind the latter the dorsum is yellowish-brown, with a white cross in the centre. The long limb of the cross is continuous with the colourless area behind the apex, and each of the short limbs lodges a vallate papilla (text-fig. 37). The frenal lamella is colourless, but the rest of the inferior surface is yellowish-brown.

The Circumvallate Papillæ (text-fig. 41 A).—Three large vallate papillæ form an equilateral triangle with the apex behind. The left basal papilla is compound, and consists of two elements; the right basal papilla is oval and excavated; and the posterior papilla is circular. The fossæ are well-marked, and the vallums form clear zones.

A fungiform papilla occupies the centre of the vallate area.

The Fungiform Papillæ (text-fig. 41 A) form a dorsal bounding zone on which they have the usual arrangement. Those lying beneath the apex are large and closely aggregated, but the transverse rows extend far forwards on the dorsum.

The Conical Papillæ (text-fig. 41 A) have the usual arrangement in clusters and rows; they increase in size in the usual manner, and their points run in the usual directions. On the pharyngeal part of the dorsum they are small and irregular. On the lateral borders and inferior surface they have the usual arrangements. All the papillæ are small or of medium size.

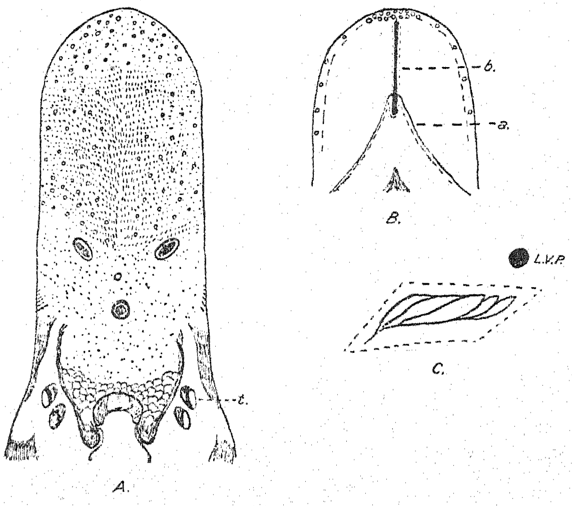
The Lateral Organs (text-fig. 41 C) extend from the dorsum to the lower parts of the edges of the tongue. Each consists of elongated fusiform laminæ running forwards and upwards, and the separating sulci are narrow. Each organ is surrounded by a diamond-shaped unpigmented area. The right organ is ·8 cm. long, and has 5 laminæ and 6 sulci. The left organ is ·7 cm long, and has 4 laminæ and 5 sulci. The dotted line in text-fig. 41 C represents the margin of the unpigmented area round the lateral organs.

Lymphoid Tissue and Glands.—The base of the tongue is delimited by a zone of large nodules with a concave anterior border. No duct orifices are visible even under a lens.

The Frenal Lamella (text-fig. 41 B, *a*).—The large, flat, triangular lamella covers a large area of the inferior surface of the tongue, and is devoid of a ridge on its upper surface. The apex is divided into small sharp processes, and the plain edges extend back to the middle of the lateral organs.

The Median Ventral Sulcus (text-fig. 41 B, *b*) lodges a well-marked crest. It opens posteriorly into a flat, shallow, unpigmented triangular area.

Text-figure 41.



The tongue of *Ateles grisescens*; *t.t.* tonsils.

The *frenum* is very short.

The *ventral papillary border* is narrow, and its papillæ have already been described.

THE BLACK-FACED SPIDER MONKEY (*A. ater*).

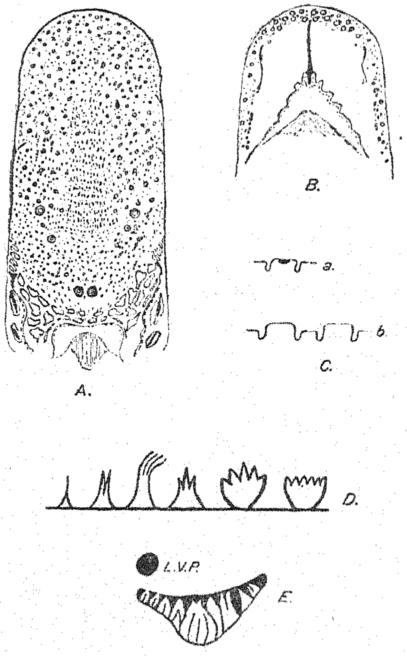
Tuckerman (**9**) described the tongue, and the following description is supplementary to his account. The *measurements* of the larger of my two specimens are:—total length 4·9 cm.; length of the oral part 4·3 cm.; length of pharyngeal part ·6 cm.; width between the lingual attachments of the palato-glossal folds 2 cm.

The Circumvallate Papillæ (text-fig. 42 A & C).—Four large papillæ form a double-pair, and two small papillæ lie on the lateral sides of the resulting rhomboid. Tuckerman states that there are three papillæ within the vallate area, but believes that they are intermediate between the fungiform and vallate groups. All the papillæ are circular, the fossæ are well-marked, and the vallums appear as clear zones. They vary in prominence, but the posterior papillæ (C, *b*) project to a greater extent than the others. All are smooth and glistening.

Only conical papillæ are seen within the vallate area.

The papillæ of the anterior pair are level with the most anterior laminæ and sulci of the lateral organs. They may be excavated (text-fig. 42 C, *a*).

Text-figure 42.



The tongue of *Ateles ater*.

The Fungiform Papillæ (text-fig. 42 A & B), which are larger than in *A. grisescens*, form a narrow dorsal bounding zone on which they have the usual arrangement. They are numerous, but small. On the inferior surface they are large; round the under surface of the apex they are closely aggregated, but farther back they are discrete (text-fig. 42 B).

Tuckerman showed how the fungiform papillæ on the under surface of the apex are richly supplied with taste-buds.

The Conical Papillæ (text-fig. 42 A) are all very small, those at the posterior part of the tongue, which are the largest, being just visible to the naked eye. They have the usual arrangement, and their distribution according to size takes the usual form. Their characters are shown in text-fig. 42 D.

They resemble the papillæ of *A. grisescens* in that those within and behind the vallate area are not regularly arranged in oblique chains.

Lymphoid Tissue and Glands.—The base of the tongue is delimited by a zone of prominent elevations, but no orifices of glands are visible. These nodules have not been mentioned by Tuckerman, who merely states that the base of the tongue is wrinkled. He describes the mucous glands, which are arranged in a small central and two lateral groups.

The Lateral Organs (text-fig. 42 E).—The prominent lateral organs form crescentic bodies on the sides of the tongue, the concavities facing the lateral vallate papillæ, which are level with the anterior laminæ and sulci. The laminæ and sulci are numerous, and are irregular in position for they have been accommodated within a small space. The right organ is ·9 cm. long, and has 9 laminæ and 10 sulci. The left organ is 1 cm. long, and has 10 laminæ and 11 sulci. Many of the laminæ have secondary sulci, and some of the primary sulci are very wide.

Tuckerman described the histology of the lateral organs.

The Frenal Lamella (text-fig. 42 B).—The triangular lamella forms a stout, thick plate with a notched apex and nodular sides. Tuckerman described a lamella, with a fimbriated edge, which possessed sensory (tactile?) end organs on its non-medullated nerves, which form a network. Gegenbaur (**11**) criticises Tuckerman's observations and thinks that the end organs are tactile in function.

The long, narrow, deep *ventral mesial sulcus* opens posteriorly into a small deep, triangular fossa. It lodges a small, median, triangular crest derived from the short frenum.

THE BLACK-HANDED SPIDER MONKEY (*A. melanochir*).

Flower (**3**) describes the tongue as follows:—"The tongue is rather lancet-shaped and pointed at the apex. The lateral group of linear follicles at the base of the palato-glossal fold is very distinct and large. The papillæ generally are soft and small. Of circumvallate papillæ there are only two, situated side by side, close to the middle line opposite the attachment of the palato-glossal folds. The frenum is attached very near (three-tenths of an inch) to the apex of the tongue, which has a stong median groove below. The sublingual papilla is rather small, soft, thick and pointed, with a slightly bifid apex."

THE RED-FACED SPIDER MONKEY (*A. paniscus*).

Mayer (**4**) described three vallate papillæ forming a triangle.

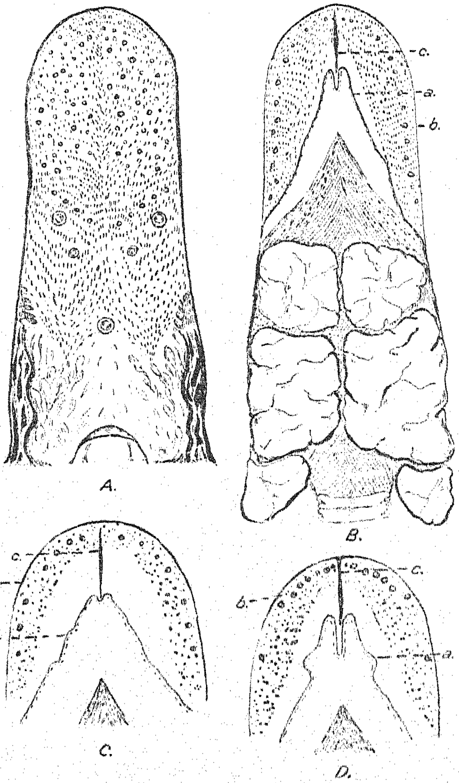
Münch (**5**) described the vallate papillæ of two specimens of *A. vellerosus*. In one there were seven papillæ on each limb, but the central papilla was absent. The central papilla was present in his second example.

Genus LAGOTHRIX.

THE SMOKY WOOLLY MONKEY (*L. infumatus*).

I examined three specimens, and the following *measurements* refer to the largest:—total length 4·6 cm.; length of the oral part 3·8 cm.; length of the pharyngeal part ·8 cm.; width between the lingual attachments of the palato-glossal folds 1·9 cm.

Text-figure 43.

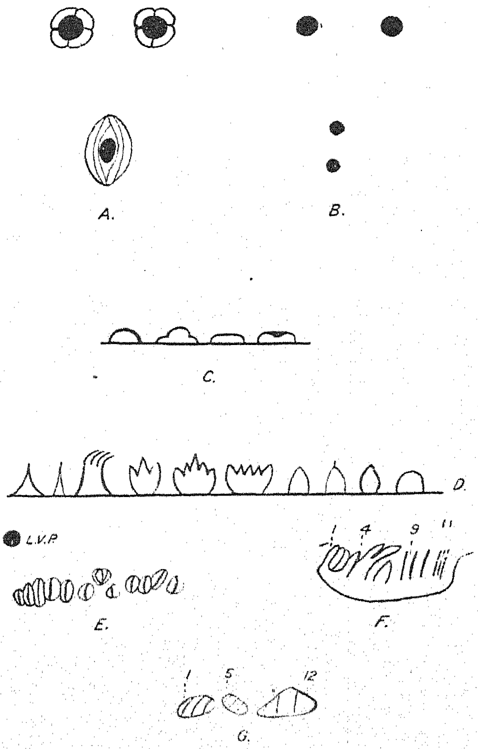


The tongue of *Lagothrix infumatus*.

Pigmentation (text-fig. 37).—The three specimens are bluish-black in colour, and the colourless fungiform and conical papillæ, renal lamella, and mesial part of the inferior surface stand out prominently from the pigmental parts. The *shape* is variable in resh specimens, being conical or oval.

The Circumvallate Papillæ (text-figs. 43 & 44 A & B).—*Specimen* No. 1 (text-fig. 43 A).—Five papillæ form a **V** with long arms. The two anterior papillæ are of medium size, the mesial papillæ are small, and the posterior papilla is large. All are prominent, smooth and colourless, the fossæ are well-marked, and the vallums appear as clear zones. The apex of the **V** is far from the epiglottis, and the anterior papillæ are close to the edges of the tongue.

Text-figure 44.



The tongue of *Lagothrix infumatus*.

Within the vallate area there are many conical papillæ, and the posterior rows of fungiform papillæ enter the mouth of the **V**.

Specimen No. 2 (text-fig. 44 A).—Three papillæ form an isosceles triangle whose equal sides are long (2 cm.), and the posterior papilla is a considerable distance from the epiglottis. The anterior papillæ are small and circular, the fossæ are well-marked, and the vallums are divided into lobes by fissures from the fossæ. The posterior papilla is oval and surrounded by a prominent furrowed vallum.

Specimen No. 3 (text-fig. 44 B).—Four vallate papillæ are arranged in the form of a **Y**, and all have well-marked fossæ and clear vallums. I do not consider that the **Y**-form in this case corresponds to that of the Simiidæ, but I believe that the papillæ of the mesial limb are members of a double-pair put into line with the long axis of the tongue.

The Fungiform Papillæ (text-figs. 43 A and 44 C).—The papillæ, which are of small and medium sizes, form a dorsal bounding zone, but the transverse rows extend as far as the apex, thereby eliminating an apical cluster. The rows contain many papillæ.

On the lateral borders and inferior surface the papillæ are small, discrete, and arranged in single chains.

All are glistening and hemispherical, and are closely surrounded by shaggy conical papillæ.

The Conical Papillæ (text-figs. 43 A and 44 D) are closely-aggregated and increase in size in the usual manner, but have no definite arrangement on the oral part of the dorsum. They are arranged in chains on the pharyngeal part of the dorsum and on the inferior surface. All are filiform, and stand up round the fungiform papillæ when the tongue is dried.

Glands and Lymphoid Tissue.—The base of the tongue is occupied by a large number of nodules, but no orifices of ducts and pits are visible. The nodules, however, are not aggregated together on a crescentic zone in front of the epiglottis.

The submaxillary and sublingual glands are enormous (text-fig. 43 B), and play the greatest part in the lubrication and softening of the food in the buccal area.

The Lateral Organs.—Specimen No. 1 (text-fig. 44 E).—The laminæ and sulci vary greatly in size, and form irregular rows on the lateral borders. The spacing between them is also very variable, for the laminæ are closely-packed posteriorly, and discrete anteriorly. Many of the laminæ are oval and traversed by wide secondary sulci.

The right organ is 1 cm. long, and has 13 laminæ and 14 sulci. The left organ is ·9 cm. long, and has 12 laminæ and 13 sulci.

Specimen No. 2 (text-fig. 44 F).—Both organs consist of long, pointed laminæ running upwards and forwards towards the lateral vallate papillæ (L.V.P), which are level with the anterior laminæ. The right organ is 1·1 cm. long, and has 11 laminæ and 12 sulci. The left organ is 1·1 cm. long, and has 12 laminæ and 13 sulci.

Specimen No. 3 (text-fig. 44 G).—The laminæ and sulci all run from behind forwards and upwards, and their white colour makes them stand out prominently against the bluish-black background of the tongue. The anterior laminæ are level with the antero-lateral vallate papillæ, and the posterior laminæ are level with the antero-mesial vallate papilla. The right organ is 1 cm. long, and has 12 laminæ and 13 sulci. The left organ is 1·1 cm. long, and has 11 laminæ and 12 sulci.

The Frenal Lamella (text-fig. 43 B *a*, C *a*, & D *a*).—The triangular lamella may have an entire or bifid apex. In the latter the halves may be long and narrow, or wide and short. The edges are plain or have processes.

The Ventral Papillary Border (text-fig. 43 B *b*, C *b*, & D *b*) is wider than in *Cebus* and *Ateles*. Its conical papillæ are in horizontal rows, but the fungiform papillæ form a single chain.

The Ventral Mesial Sulcus (text-fig. 43 B *c*, C *c*, D *c*) may be narrow and deep, or wide and shallow. It has no mesial crest.

Humboldt's Woolly Monkey (*L. humboldti*).

The tongue has three vallate papillæ forming an isosceles triangle; of these the apical one is large. The fungiform papillæ are large and conspicuous, and have the usual arrangement in clusters and rows. The triangular frenal lamella has a bifid apex.

Genus Saimiris (=Chrysothrix).

The Squirrel Monkey (*S. sciurea*).

Measurements:—total length 2·1 cm.; length of the oral part 1·9 cm.; length of the pharyngeal part ·4 cm.; width between the lingual attachments of the palato-glossal fold 1·1 cm.

The Circumvallate Papillæ.—Three papillæ form an isosceles triangle with the apex behind. The right basal papilla is strongly retracted within its fossa, but the others are prominent, granular, and surrounded by nodulated vallums.

The Conical and Fungiform Papillæ have the usual arrangement, and the latter form a dorsal bounding zone.

Glands and Lymphoid Tissue are present as usual on the base of the tongue, but no duct orifices are visible.

Both *lateral organs* are 5 cm. long, and have five primary sulci separating four laminæ; the latter are traversed by secondary sulci. Each organ appears as a straight line of laminæ and sulci.

The *frenal lamella*, as shown by Pocock, is long, narrow, and has a slightly divided apex. The *frenum* is long.

Genus Callicebus.

The Moloch Teetee (*C. moloch*).

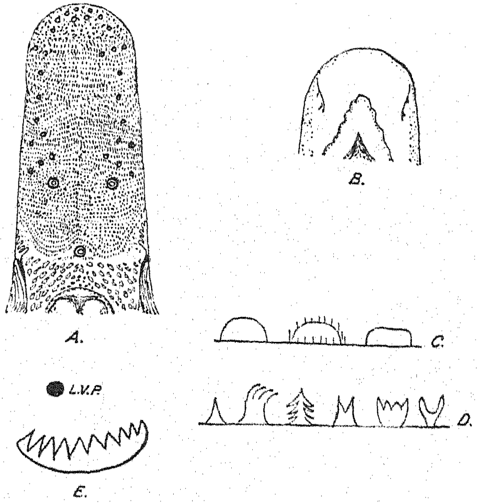
Three specimens were examined, and the *measurements* were very similar in all. The following figures refer to my largest example:—total length 2·55 cm.; length of the oral part 2·15 cm.; length of the pharyngeal part ·4 cm.; width between the lingual attachments of the palato-glossal folds 1·2 cm.

The tongue is bluish-black in colour on the entire oral part and on most of the pharyngeal part of the dorsum. The inferior surface has a bluish-black bounding zone. The frenal lamella, mesial part of the inferior surface, and cuneiform areas on the base of the tongue are unpigmented, and the vallate and fungiform papillæ may or may not be colourless; in the former case the appearance of the dorsum resembles that of *Lagothrix infumata* (text-fig. 37).

The Circumvallate Papillæ (text-fig. 45 A).—Three papillæ form an isosceles triangle with long sides, and an acute vertical angle. The posterior papilla is granular and projects considerably beyond the coarsely-nodulated vallum. The right basal papilla is granular, and the vallum is overlapped by conical papillæ. The left basal papilla is round, granular, and pigmented.

The Fungiform Papillæ (text-fig. 45 A & C) form a narrow dorsal bounding zone on which they have the usual arrangement, but the transverse rows extend far forwards. Those on the inferior surface are minute and form a single row. Some are overlapped by conical papillæ.

Text-figure 45.



The tongue of *Callicebus moloch*.

The Conical Papillæ (text-fig. 45 A & D) are all shaggy, and stand up around the fungiform papillæ when the tongue is dried. The rows are mostly transverse, but the distribution according to size is not according to the typical plan. All the papillæ are of the filiform types.

Lymphoid Nodules and Glands.—The base of the tongue is occupied by nodules, but no orifices of ducts of glands are visible.

The Lateral Organs (text-fig. 45 E).—The wide primary sulci appear as incisions on the lateral borders, for the intervening laminæ are flat. They form a slightly concave row whose posterior members are level with the lateral vallate papilla (L.V.P.).

The entire organ is surrounded by an oval colourless area of the tongue, so they offer a marked contrast to the bluish-black lateral borders.

The right organ is ·6 cm. long, and has 10 laminæ and 11 sulci. The left organ is ·5 cm. long, and has 9 laminæ and 10 sulci.

The *Ventral Papillary Zone* is bluish-black and narrow. It has many small irregularly-placed conical papillæ, and a few fungiform papillæ in a single row posteriorly.

The *Ventral Mesial Sulcus* is narrow and deep, and the *frenal lamella* is triangular and entire with lobulated edges.

THE BROWN TEETEE (*C. brunnea*).

In a hitherto unpublished paper Garrod states: "There are three circumvallate papillæ in the form of a triangle. The fungiform papillæ are most numerous at the tip of the tongue, and there are a few in front of the circumvallate papillæ and Mayer's Organ. There is a good bifid sublingua" (=frenal lamella).

Owen (**6**) described a vallate triangle in *C. personata*.

Genus AOTUS (=NYCTIPITHECUS).

THE FELINE DOUROUCOULI (*A. felinus*).

The two specimens which I examined were preserved, so no measurements were made. One of them has a single vallate papilla.

The *apex* and *lateral borders* have the usual characters, and a well-marked *mesial dorsal sulcus* runs along the base of the tongue.

The Circumvallate Papillæ (text-fig. 46 A & C).—Two prominent vallate papillæ lie near the lateral borders. Each is granular, and has a prominent nodular vallum. The fossæ are well-marked. Both are round on plan and on conical elevation.

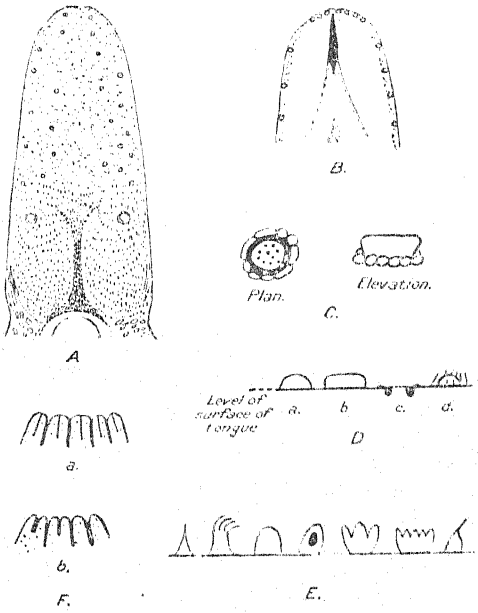
The Fungiform Papillæ (text-fig. 46 A & D) form a dorsal bounding zone on which they have the usual arrangement. Some are flush with the general surface of the tongue (*c*), but others stand up prominently (*a* & *b*). They form a single row on the ventral surface of the tongue, and some are overlapped by conical papillæ (*d*).

The Conical Papillæ (text-fig. 46 A & E) have the usual distribution according to size, and the usual direction of their points. They do not have the usual arrangement, however; on the oral part of the dorsum they are irregular, but on the base they form oblique chains. They are cylindrical or filiform, and may have central depressions.

The Lateral Organs (text-fig. 46 F).—The laminæ and deep narrow primary sulci lie on the edges and the inferior surface of the tongue. They run forwards and upwards, and the laminæ are traversed by secondary sulci. The right organ is ·9 cm. long, and has 5 laminæ and 6 sulci. The left organ is ·8 cm. long, and has 4 laminæ and 5 sulci.

The Inferior Surface (text-fig. 46 B).—The narrow *ventral papillary zone* has irregularly disposed conical papillæ and a single row of discrete prominent fungiform papillæ; the latter are most numerous and closest together round the apex.

Text-figure 46.



The tongue of *Aotus felinus*.

The *frenal lamella* is triangular. It has a bifid apex and plain sides. The *ventral mesial sulcus* is shallow and deep, and the *frenum* is of moderate length.

Genus Pithecia.

The Black Saki (*P. satanus*).

The specimen which I examined was preserved, so no measurements were made.

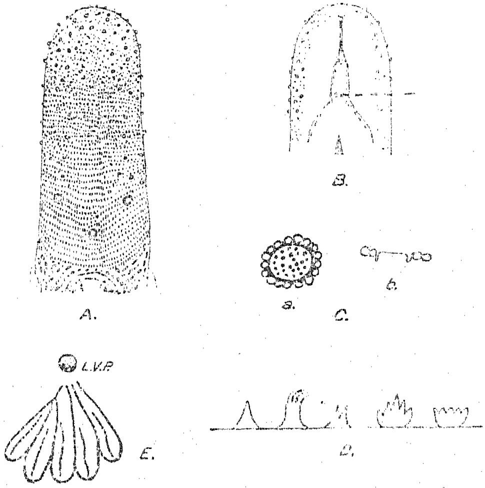
The tongue has almost parallel sides, and the *apex* and *lateral borders* have the usual characters. The thickness rapidly diminishes from frenal lamella to apex.

The Circumvallate Papillæ (text-fig. 47 A & C).—The vallate papillæ form an isosceles triangle with the apex behind. All are slightly retracted, with granular surfaces, the fossæ are well-marked, and the vallums are nodulated.

The Fungiform Papillæ (text-fig. 47 A & B) form a dorsal bounding zone on which they have the usual arrangement, and the apical cluster is very well-marked. They form a single row on the inferior surface. They are all prominent, smooth, and hemispherical, and none are overlapped by conical papillæ.

The Conical Papillæ (text-fig. 47 A & D) have the usual arrangement in clusters and rows of varying degrees of obliquity. The vertical direction of the rows on the lateral borders can only be made out by very careful examination, however. All belong to the filiform series.

Text-figure 47.



The tongue of *Pithecia satanas.*

The Lateral Organs (text-fig. 47 E) form triangular or concave bodies on the sides and inferior surface, and the lateral vallate papillæ are level with the apex. Several of the pointed laminæ have secondary sulci. The right organ is ·9 cm. long, and has 5 laminæ and 6 sulci. The left organ is ·8 cm. long, and has 4 laminæ and 5 sulci.

The Inferior Surface (text-fig. 47 B).—The broad *bounding papillary zone* is wide, and has papillæ disposed in the usual manner.

The *frenal lamella* is a long plate with rounded apex, and the orifices of the Wharton's Ducts open on the ventral surface near the base (text-fig. 47 B, *a*).

The *ventral mesial sulcus* is wide and deep, and the *frenum* is short.

Mayer described a vallate triangle in *P. satanas* (4).

HUMBOLDT'S SAKI (*P. monachus*).

Flower (3) describes the tongue as follows:—"The length of the tongue, from the base of the epiglottis to the tip, is 1·4 inch; its breadth ·5 inch; its sides are parallel, the end square, with the corners slightly rounded. The sublingual organ is fleshy, except towards the end, which is sharp-pointed and cleft at the extreme tip; it is free to the extent of ·25 inch, and its apex is ·3 from the tip of the tongue."

In a hitherto unpublished note Garrod states that the tongue of *Pithecia albinasa* has a triangular vallate papillary area.

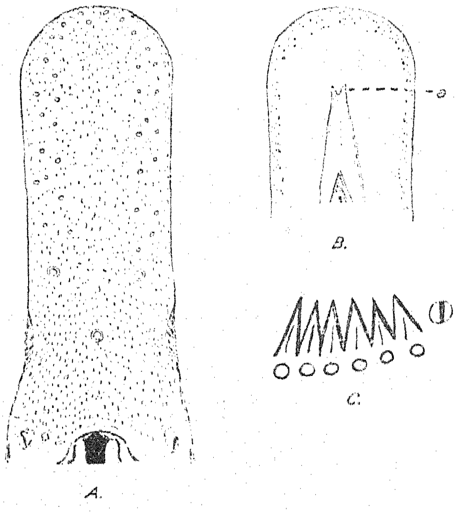
Genus CACAJAO.

THE BALD OUAKARI (*C. calva*).

The specimen had been preserved, so no measurements were made.

The *apex* and *lateral borders* have the usual characters, but fine lateral striæ, only visible on high magnification, run in from them across the dorsum.

Text-figure 48.



The tongue of *Cacajao calva*.

The Circumvallate Papillæ (text-fig. 48 A).—Three vallate papillæ form an isosceles triangle whose apical papilla is far from the epiglottis; the basal papillæ are close to the edges of the tongue. The apical papilla is small and the basal ones large, the fossæ are all well-marked and the vallums are nodular.

The Fungiform Papillæ (text-fig. 48 A & B) form a dorsal bounding zone on which they have the usual arrangement in clusters and rows, but the apical cluster is small. Nowhere are they numerous, however. They are absent from the inferior surface.

The Conical Papillæ are irregularly arranged, but they increase in size in the usual manner and their points run in the usual directions. They form a narrow papillary zone on the inferior surface, but this is widest round the apex.

Glands and Lymphoid Tissue.—The base of the tongue is finely nodular, and a few orifices are visible when it is highly magnified.

The Lateral Organs (text-fig. 48 C) form concave bodies on the sides of the tongue, and the pointed or round laminæ have fungiform papillæ below their bases. The lateral vallate papillæ are level with the centres of the organs. All rounded laminæ have wide secondary sulci.

The right organ is 1 cm. long, and has 7 laminæ and 8 sulci. The left organ is ·9 cm. long, and has 6 laminæ and 7 sulci.

The Inferior Surface (text-fig. 48 B).—The *ventral papillary zone* is narrow, the *ventral median sulcus* is shallow, and the frenum is small.

The *frenal lamella* is long and narrow, and terminates in two small points (text-fig. 48 B, *a*).

Genus ALOUATTA (= MYCETES).

THE BLACK HOWLER MONKEY (*A. caraya*).

The specimen had been preserved, so no measurements were made.

The Circumvallate Papillæ (text-fig. 49 A & C).—Three papillæ form an isosceles triangle with long sides. The apical papilla is far from the epiglottis, and the basal papillæ are close to the lateral borders of the tongue. The length of the vallate triangle is one-third the length of the dorsum.

The apical papilla is large, oval, granular, and excavated in the centre, the fossa is well-marked, and the vallum striated.

The Fungiform Papillæ (text fig. 49 A & B) are not numerous, but have the usual arrangement on the dorsum; and a few lie at the sides of the vallate triangle. They appear to stand on ridges of the mucosa when the tongue is highly magnified. Those on the inferior surface are very small.

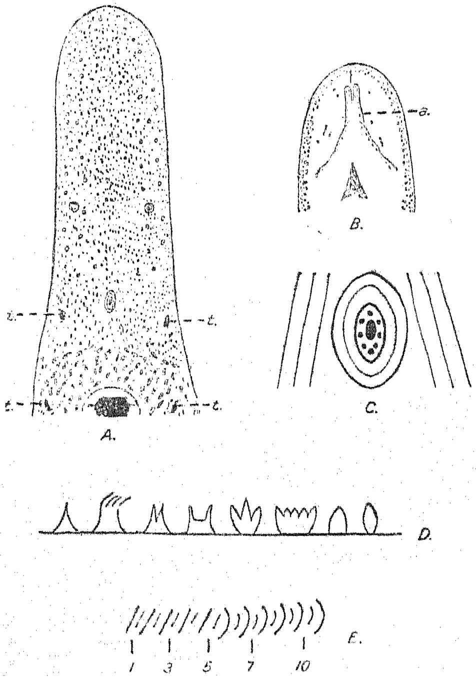
The Conical Papillæ (text-fig. 49 A, B, & D), which are closely-set, are irregularly disposed on the dorsum, but they increase in size in the usual manner, and their points run in the usual direction. They are filiform, cylindrical, or fusiform, and the number of points to each papilla varies. Some stand up so prominently round the fungiform papillæ that they conceal them entirely.

Glands and Lymphoid Tissue (text fig. 49 A).—The base of the tongue is covered with nodules of various sizes, and many orifices of ducts are visible to the naked eye. The lens reveals the existence of many minute openings, and the base of the tongue is more pitted than in other species of the Cebidæ. Many nodules with central depressions are also present on the anterior surface of the epiglottis.

The Lateral Organs (text-fig. 49 E).—On each side they form a straight row of laminæ and sulci. All the sulci and laminæ are short; the posterior ones are straight, and the anterior ones, which are level with the anterior vallate papillæ, are convex forwards.

The right organ is ·9 cm. long, and has 10 laminæ and 11 sulci. The left organ is ·7 cm. long, and has 8 laminæ and 9 sulci.

Text-figure 49.



The tongue of *Alouatta caraya*; *t. t.* tonsils.

The Inferior Surface (text-fig. 49 B).—The *ventral papillary zone* is narrow, but has papillæ disposed in the usual manner.

The *ventral mesial sulcus* is short, but does not open up much when traced posteriorly.

The *frenum* is short, and the *frenal lamella* is long, narrow, deeply incised at the apex, and has plain sides (text-fig. 49 B, *a*).

Carus and Otto (1) described a vallate triangle (*A. fuscus*) closely resembling that of *A. caraya*, described above.

Summary of the Tongues of the Cebidæ.

1. All tongues, except those of the Sakis, are conical, and some are pigmented.
2. The conical papillæ are irregularly disposed on the oral part of the dorsum in most of the Cebidæ, but they may be arranged in chains on the base of the tongue.
3. The fungiform papillæ always form a dorsal bounding zone. They may be absent from the inferior surface.
4. The vallate papillary patterns are—a single papilla, a pair, a triangle, a V, or a double-pair.
5. The vallate triangle is far from the epiglottis in many species, and its median may be very long (the median is the line drawn from the apex to the mid-point of the base).
6. The orifices of the ducts of glands are fewer than in the Cercopithecidæ. They are most marked in *Alouatta*.
7. The lateral organs are most frequently concave towards the epiglottis.
8. The frenal lamella is usually bifid at the apex.
9. The lingual characters are not sufficiently distinctive to be of value for the classification of species.

Family Hapalidæ.

Genus Hapale.

The Common Marmoset (*H. jacchus*).

The comparatively long, slender tongue has the following *measurements*:—total length 2·1 cm.; length of the oral part 1·9 cm.; length of the pharyngeal part ·2 cm.; width between the lingual attachments of the palato-glossal folds ·65 cm. These figures were found to be the average in twelve specimens.

The *apex* is flat and tuberculated by fungiform papillæ; it is devoid of a notch. Running back for 1 cm. is a *median dorsal sulcus* from which transverse sulci pass to the sides of the tongue, but these are the result of preservation and are not shown in text-fig. 50. The *lateral borders* have the usual characters.

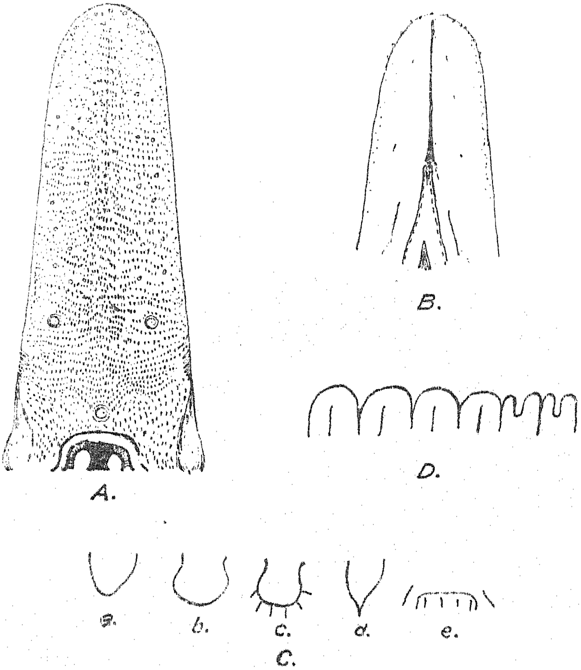
The Circumvallate Papillæ (text-fig. 50 A).—Three vallate papillæ form an isosceles triangle with the apex behind, and the two basal papillæ are close to the edges of the tongue. The vallums are covered by conical papillæ which obscure the fossæ, and the surfaces of the papillary bodies are finely granular. This pattern was present in all twelve specimens. Tuckerman (**9**) also described this as the type.

The Fungiform Papillæ (text-fig. 50 A & B) form a dorsal bounding zone on which they have the usual arrangement, in clusters and rows, and they are surrounded by prominent upstanding conical papillæ. They are few in number, however, on the dorsum, and are absent from the ventral bounding papillary zone.

The Conical Papillæ (text-fig. 50 A, B, & C) have an irregular disposition, but they increase in size in the usual manner, and their points run in the usual directions. They appear as imbricated scales, and some stand up prominently round the fungiform and vallate papillæ, concealing the vallums of the latter (text-fig. 50 C, *e*).

Lymphoid Tissue and Glands.—A few nodules are present among the conical papillæ on the base of the tongue, but no duct orifices are visible.

Text-figure 50.



The tongue of *Hapale jacchus.*

The Lateral Organs (text-fig. 50 D).—These consist of a few fine laminæ and sulci on the sides of the tongue. The right one has 6 laminæ and 7 sulci, and the left one has 5 laminæ and 6 sulci. Some of the laminæ have small secondary sulci.

The Inferior Surface (text-fig. 50 B).—A narrow *ventral papillary border*, possessing conical papillæ only, is present, and the narrow, deep ventral mesial sulcus opens posteriorly into a triangular fossa.

The *frenal lamella* is triangular, with a bifid apex and plain or nodulated sides.

THE BLACK-EARED MARMOSET (*H. penicillata*).

The conical tongue, which is green in colour, has the following *measurements*:—total length 2·35 cm.; length of the oral part 2·1 cm.; length of the pharyngeal part ·25 cm.; width between the lingual attachments of the palato-glossal folds ·9 cm.

The *apex* is pointed and tuberculated; running backwards from 1·4 cm. is a median ridge, whence transverse ridges, which are convex forwards, run out to the lateral borders.

The Circumvallate Papillæ.—Three papillæ form an isosceles triangle. The apical papilla is close to the epiglottis, and the lateral papillæ are close to the edges of the tongue. The lateral papillæ are small, and their fossæ and vallums are concealed by conical papillæ (text-fig. 51 A, *b*). The posterior papilla, which is oval and excavated, has a nodulated vallum composed of two rows of lobules (text-fig. 51 A, *c*).

The Fungiform Papillæ form a wide dorsal bounding zone, and the area of the centre without papillæ is small. They have the usual arrangement, but the posterior rows form thick clusters in front of the vallate papillæ. They are hemispherical or flat, and the surfaces are smooth and glistening. As in *H. jacchus*, there are none on the inferior surface of the tongue.

The Conical Papillæ have the usual arrangement, but their size remains the same from apex to base. They are scale-like and imbricating, as in *H. jacchus*. They form a narrow zone on the inferior surface of the tongue (text-fig. 51 A, *a*).

Lymphoid Tissue and Glands.—The area occupied by the lymphoid nodules is small, and no duct orifices are visible.

The *lateral organs* consist of a few very fine laminæ and sulci. It is difficult to detect these, even on high magnification, by a hand lens, so microscopical examination is necessary in order to settle their characters.

The Inferior Surface (text-fig. 51 A, *a*).—A narrow *ventral papillary border* is present; the narrow, deep *ventral mesial sulcus* opens posteriorly into a triangular fossa; and the *frenal lamella* is triangular, with an entire apex and notched sides.

THE PYGMY MARMOSET (*H. pygmæa*).

The tongue has the following characters:—

1. It is conical with a rounded apex.
2. The vallate papillæ form an isosceles triangle.
3. The fungiform papillæ resemble those of *H. penicillata*.
4. The conical papillæ form imbricating scales.
5. The lateral organs are well-marked.
6. The ventral papillary zone is well-marked.
7. The ventral mesial sulcus is long and deep.
8. The triangular frenal lamella has a bifid apex.

Genus Leontocebus.

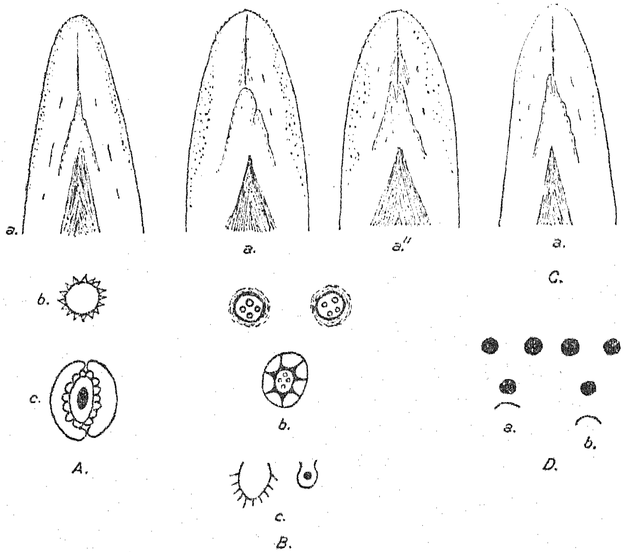
The Lion Marmoset (*L. rosalia*).

The two specimens examined were preserved, so no measurements were taken.

The tongue rapidly tapers from base to apex; and the latter is pointed and covered with a dense cluster of small fungiform papillæ. The middle of the dorsum is occupied by a strip of mucosa covered by closely-aggregated conical papillæ.

The Circumvallate Papillæ (text-fig. 51 B, *b*).—Three papillæ form an isosceles triangle with two short sides and a long base.

Text-figure 51.



The inferior surfaces of the tongue and vallate papillæ of some Marmosets.

The apical papilla is a short distance anterior to the epiglottis, and the basal papillæ are close to the edges of the tongue.

All the papillæ are large and nodulated, the fossæ are well-marked, and the vallums are clear zones or lobulated bands.

The Fungiform Papillæ, which are prominent, form a well-marked dorsal bounding zone on which they have the usual arrangement in clusters and rows, and they increase in size in the usual manner. Two rows of small elements connect the basal vallate papillæ. None are present on the posterior part of the ventral papillary zone.

All are prominent, hemispherical, and smooth.

The Conical Papillæ (text-fig. 51 B, *c*).—No apical cluster is present, for the transverse rows extend right forward to the apex.

Each is leaf-shaped, and has several hair-like processes along its free edge, and all the points are directed backwards. Some of the posteriar papillæ may be umbilicated. They increase in size in the usual manner.

Lymphoid Tissue and Glands.—The nodules form a narrow zone in front of the epiglottis, but no duct orifices are visible, even through the lens.

The Lateral Organs.—The lateral organs consist of well-marked, but small, backwardly-directed laminæ separated by deep primary sulci. The right organ has 3 laminæ and 4 sulci, and the left organ has 4 laminæ and 5 sulci.

The Inferior Surface (text-fig. 51 B, *a* & *a''*).—No *ventral papillary zone* is present, but the outer part of the inferior surface incised by small fissures.

The *ventral mesial sulcus*, which is narrow and deep, opens posteriorly into a large triangular space.

The *frenum* is short, and the *frenal lamella* is triangular, with a bifid apex, or a deep notched lateral border.

Genus Mystax.

The Negro Tamarin (*M. ursulus*).

My fresh specimen has the following *measurements*:—total length 2·8 cm.; length of the oral part 2·4 cm.; length of the pharyngeal part ·4 cm.; width between the lingual attachments of the palato-glossal folds 1·2 cm.

The *apex* is rounded, and a *dorsal median sulcus*, which is more marked than in any specimen belonging to the Cercopithecidæ, Cebidæ, or Hapalidæ, runs back to the apex of the vallate triangle. No transverse ridges or sulci are present.

The Circumvallate Papillæ (text-fig. 52 A. & C).—Four papillæ are arranged in the form of a **V**. Including the apical papilla the right limb has three papillæ and the left one has two. The posterior papilla (A, C *a*) is oval, with a well-marked fossa and nodular vallum. The left lateral papilla (A, C *b*) lies in a wide fossa with three small ones. The right lateral papilla (A, C *c*) lies in a wide fossa with two small ones, and the right mesial papilla is circular.

The Fungiform Papillæ (text-fig. 52 A & B).—Small, but well-marked papillæ form a dorsal bounding zone, but the transverse rows are maintained as far forwards as the apex. They are absent from the inferior surface.

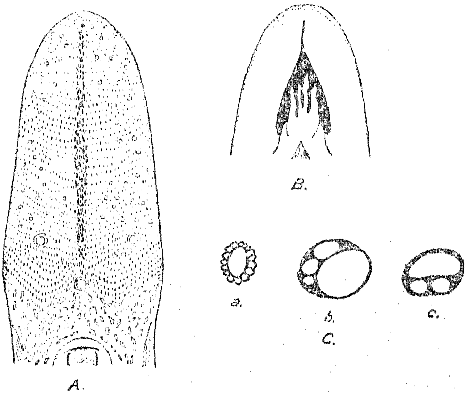
The Conical Papillæ,—No apical cluster is present, for the papillæ maintain their arrangement in rows right forward to the apex, and there is no great increase in size from before-backwards, or without-inwards. They have the usual arrangement on the ventral papillary zone. All are cylindrical and surrounded by zones of interpapillary dorsum.

Lymphoid Tissue and Glands.—On each side of the epiglottis there is a large nodular mass, and the two are connected by a band of small nodules which also passes towards the posterior vallate papilla. Some of the large nodules have small central pits.

The Lateral Organs.—The laminæ, which increase in size from before backwards, are separated by wide primary sulci. The right organ has 3 laminæ and 4 sulci, and the left one has 4 laminæ and 5 sulci.

The Inferior Surface (text-fig. 52 B).—The *ventral papillary border*, which is narrow, possesses conical papillæ only.

Text-figure 52.



The tongue of *Mystax ursulus.*

The *ventral mesial sulcus*, which is long, narrow, and deep, opens posteriorly into a large triangular depression containing a well-marked median crest.

The *frenal lamella* is a long, flat body with its anterior extremity deeply cleft into several long, thin club-like processes.

THE MOUSTACHE TAMARIN (*M. mystax*).

The tongue, whose form resembles those of the preceding species, has the following *measurements* :—total length 2·1 cm.; length of the oral part 1·8 cm.; length of the pharyngeal part ·3 cm.; width between the lingual attachments of the palato-glossal folds ·6 cm.

A deep *median dorsal sulcus* runs back for 1·1 cm. from the apex, and *transverse furrows* run towards the lateral borders; these separate broad ridges which are convex forwards and concave backwards.

The Circumvallate Papillæ.—Three papillæ form an isosceles triangle with two short sides and a long base; the apical papilla is close to the epiglottis, and the basal papillæ are close to the lateral borders of the tongue.

All are round and finely-granular, the fossæ are well-marked, and the vallums are lobulated.

The Fungiform Papillæ, which are all small but prominent, form a dorsal bounding zone on which they have the usual arrangement in clusters and rows, the usual number on each row being two. Most of them are equal in size, and are smooth and hemispherical.

The Conical Papillæ, which are all closely-aggregated, have the usual arrangement in rows and clusters; they increase in size from without-inwards, but their increase in size from before-backwards is slight. They take the form of overlapping scales with hair-like processes.

Lymphoid Tissue and Glands.—The nodular zone on the base of the tongue is narrow, and no orifices of ducts and pits are visible, even when the tongue is highly magnified.

The Lateral Organs are small and oval: their centres are level with the lateral vallate papillæ. They consist of well-marked primary sulci separating comparatively broad laminæ with pointed or rounded upper extremities. The secondary sulci are very thin.

The right organ is ·1 cm. long, and has 3 laminæ and 4 sulci. The left organ is ·1 cm. long, and has 4 laminæ and 5 sulci.

The Inferior Surface.—The narrow *ventral papillary zone* has only conical papillæ, but is incised by transverse sulci running in from the dorsum.

The *ventral mesial sulcus*, which is narrow and deep, opens into a large triangular space, which also receives the short frenum.

The *frenal lamella* is triangular, with a bifid apex and fissured lateral borders.

Genus Œdipomidas.

The Pinche Monkey (*Œ. œdipus*).

Flower (3) described the tongue and gave the following data:—

1. The tongue tapers gradually.
2. There is a median dorsal sulcus posteriorly.
3. The ventral median sulcus is deep.
4. The fungiform papillæ are regular, and cover the entire oral part of the dorsum.
5. Three vallate papillæ form a triangle.
6. The lateral organs are well-marked.
7. The frenal lamella has a dorsal ridge and cleft apex.

Summary of the Tongues of the Hapalidæ.

1. The tongue is either long, narrow, and tapering slowly, or short, conical, and tapering rapidly from a wide base.
2. Mesial dorsal ridges are frequently present.
3. The tongue of *Mystax ursulus* has a better-marked mesial dorsal sulcus than those of all other Primates.

4. The vallate papillæ always form a triangle.

5. The fungiform papillæ always form a dorsal bounding zone.

6. Scale-like conical papillæ, with or without filamentous processes, are exceedingly common.

7. The ventral papillary zone is small or absent.

8. The frenal lamella is usually subdivided at the apex, but undivided lamellæ occasionally appear.

9. The lateral organs are always small.

10. The lytta, foramen cæcum, plicæ, fimbriatæ, and apical gland of Nuhn are absent.

BIBLIOGRAPHY.

1. CARUS and OTTO.—Erläuterungstafeln zur vergl. Anatomie. Heft 4. Leipzig, 1835.
2. CUVIER.—Leçons d'Anatomie comparée. Paris: Crochard et Cie., 1835.
3. FLOWER, W. H.—Medical Times and Gazette, 1872, vol. i. pp. 507–509; and Proc. Zool. Soc. London, 1862, p. 331.
4. MAYER, F. J. C.—See Bibliography to paper No. 8.
5. MÜNCH.—See Bibliography to paper No. 8.
6. OWEN, R.—The Comparative Anatomy of the Vertebrata, vol. iii. p. 199.
7. PODWISOTSKY, V.—"Anat. Untersuch. über die Zungendrüsen des Menschen und der Säugethiere." Diss. Dorpat, 1878.
8. SONNTAG, C. F.—"The Tongues of the Cercopithecidæ." Proc. Zool. Soc. London, 1921, pp. 277–322.
9. TUCKERMAN, F.—Journal of Anatomy and Physiology, 1892, pp. 391–392.
10. BOULART and PILLIET.—See Bibliography to paper No. 8.
11. GEGENBAUR, C.—Morphol. Jahrbuch. 1894, pp. 1–18.
12. POCOCK, R. I.—Ann. Mag. Nat. Hist. (8) xx. pp. 247–258.

28. Note on the Skull of *Dinotherium giganteum* in the British Museum. By C. W. Andrews, D.Sc., F.R.S., F.Z.S.

(Submitted for Publication by permission of the Trustees of the British Museum.)

[Received March 5, 1921: Read May 24, 1921.]

(Text-figures 1–4.)

One of the most important specimens in the Geological Department of the British Museum is the fine skull of *Dinotherium giganteum*, which seems to be the only even approximately complete example at present known. The history of this specimen is of considerable interest. It was discovered in 1835 by Klipstein, about eighteen feet deep in the well-known ossiferous sands of Eppelsheim in Hesse-Darmstadt. An account of this discovery, including a description of the specimen and of the deposits in which it occurred, was published by Klipstein and Kaup in 1836 under the title "Beschreibung und Abbildungen von dem in Rheinhessen gefundenen colossalen Schädel des *Dinotherii gigantei*": in the following year a French translation of this paper appeared. Kaup, in his part of the memoir, not only gives a description of the skull itself, but also a very interesting account of the method of collecting the specimen. It appears that it was found lying on its dorsal surface in a bed of clay and sand. This was partly removed, leaving the skull resting on six pillars of matrix. Next, iron bars were passed through the openings thus made, which were then filled up with plaster of Paris. Next, the remaining portions of the matrix were removed and their place filled with more plaster, so that finally the skull rested on a solid base of plaster strengthened by iron bars. A stout board was inserted beneath the whole mass, which was then lifted from the excavation by twenty-four men with ropes. A quaint picture of this operation is given on the cover of Klipstein and Kaup's memoir. In this figure there is also shown a huge proboscidean femur, which is perhaps the original from which the cast of a Dinotherium femur now in the British Museum was made. In 1837 the skull was sent to be exhibited in Paris, part of the expenses of transport being borne by the French Academy. While there it was examined by de Blainville, whose description of the specimen is the best yet published; but even he was not allowed any opportunity of examining the dorsal surface. On the same occasion Isidore Geoffroy, Straus, and others took the opportunity of giving their views as to the structure and affinities of *Dinotherium*. It was then intended to send the specimen to London, but whether this was done on this occasion is uncertain. Some years later, in 1849, it was certainly in London, and was offered to the British

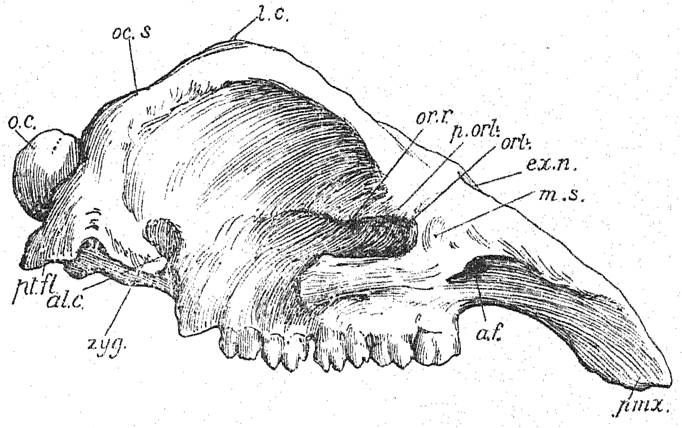
Museum for purchase; it was then examined and reported on by Buckland and Owen. The purchase was not completed, and the skull seems to have been sent back to Darmstadt. About 1866, Klipstein sold his collection to Dr. Oldham, the Director of the Geological Survey of India, and from him the British Museum acquired not only this, but also some other valuable specimens, including the skull of *Dorcatherium naui* and the front of the skull of *Tapirus priscus*.

Dr. W. D. Mathew, when visiting the Museum recently, pointed out to me that there is a widely-spread idea on the Continent that the skull now under discussion was broken up on its journey to London. This mistake has even appeared in print: thus Weinsheimer in his memoir on *Dinotherium* (Pal. Abhandl. Bd. i. 1883, p. 244), in speaking of the cast of this specimen, states that "The original of this cast no longer exists, since on its journey to London it was irretrievably broken into fragments." Examination of the skull shows that, in fact, at some time it has been much broken, but has been, on the whole, skilfully mended, the figures and cast no doubt having been followed in making the restoration.

In addition to Kaup's original descriptions and figures, de Blainville has given a very good account of the skull so far as he was able to examine it, and numerous other writers have referred to it. The most complete summary of the various views that have been held as to the affinities of *Dinotherium* is given by Stefanescu in his paper on *Dinotherium gigantissimum* (Anuarulu Museului de Geologia, etc., Bukarest, 1894, p. 126). It is now proposed to give a short description of the skull as it now is, followed by some discussion of the reasons for its peculiarities and of the relationships of *Dinotherium* to the other Proboscidea.

The occipital condyles (*o.c.*) are very large and prominent; ventrally and laterally they are limited by a deep groove, but dorsally they seem to pass uninterruptedly into the occipital surface (*oc.s.*). The articular surface of the condyles from above downwards makes rather more than a semicircle, so that the range of movement of the head up and down was extensive. Ventrally the condyles are separated by a broad, deep notch, in front of which the basioccipital runs downwards and forwards as a broad ridge, narrowing a little towards its junction with the basisphenoid, at which point. however, there is a prominence. The basisphenoid is not quite in the same straight line as the basioccipital, but seems to have been directed a little more upwards. The basis cranii as a whole slopes rather steeply downwards, making an angle of about 135 degrees with the plane of the teeth and the posterior part of the palate, which is regarded as being horizontal. From the outer angle of each condyle a ridge (*r.*) runs outwards and a little upwards, terminating in the outer angle of the squamosal (*a.s.*), which projects outwards far beyond the level of the zygomatic processes. These ridges, which towards their outer ends rise into thick and prominent crests, separate the upper occipital surface from the large post-tympanic flanges (*pt.fl.*), which appear to be formed partly by the exoccipitals and partly by the squamosal, though no suture can be seen; the angle between the post-tympanic flanges and the upper occipital surface is about 130 degrees. The ventral border of the flanges is gently convex, and is separated from the condyles on the inner side by a deep notch, which is partly occupied by a tongue-like process of bone, apparently the paroccipital process (*p.p.*) of the exoccipital. The anterior face of the flanges is concave from side to side, and is separated superiorly from the greatly elongated glenoid surface (*gl.*) for the mandible by a shallow transverse channel. Above the transverse ridges just described the occipital surface slopes forwards to a remarkable degree, giving the skull a curious resemblance, in this region, to the skull of some types of Whales, e. g. *Balænoptera*. The angle between the occipital surface and the basis cranii is about 53 degrees, so that the occiput is nearly parallel to the palatal surface. This extraordinary forward inclination of the occiput evidently limits the size of the cranial cavity, and de Blainville suggested that possibly the occipital surface had been crushed down towards the floor of the skull. Careful examination of the specimen, however, does not seem to support this idea, and it seems probable that, remarkable as the

Text-figure 1.



Skull of *Dinotherium giganteum*.
From right side: about $\frac{1}{15}$ nat. size.

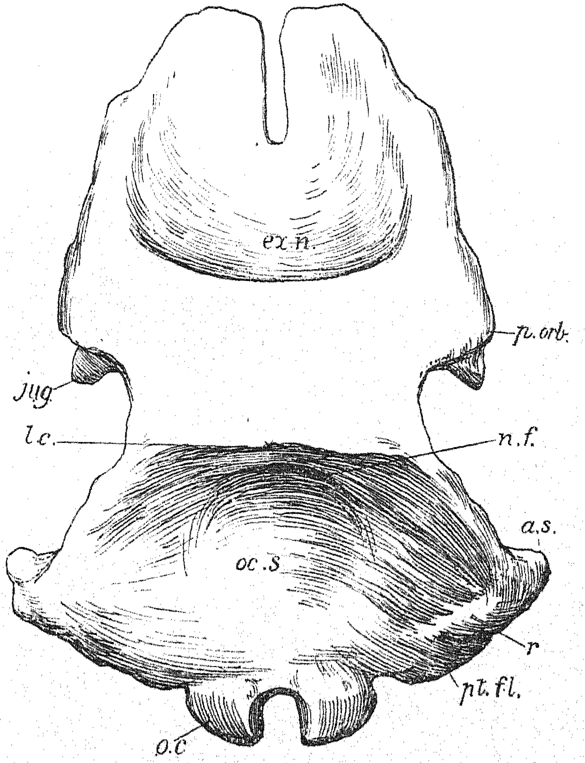
a.f., antorbital foramen; *al.c.*, posterior opening of alisphenoid canal; *ex.n.*, external nares; *l.c.*, lambdoidal crest; *m.s.*, depression for muscle attachment on preorbital prominence; *o.c.*, occipital condyle; *oc.s.*, occipital surface; *orb.*, orbit; *or.r.*, orbital ridge; *pmx.*, premaxilla; *p.orb.*, post-orbital process of frontal; *pt.fl.*, post-tympanic flange; *zyg.*, zygomatic process of squamosal.

structure of this region of the skull may appear, it represents nearly the condition in the living animal. In other Proboscidea the occiput slopes strongly forwards, but this inclination is masked, in the adult at least, by the enormous development of cellular bone that takes place in this region, except over the area of the insertion of the ligamentum nuchæ, which occupies in consequence a deep depression.

In young individuals in which this development of the bone has not taken place, it can be seen that the occiput is inclined to the basis cranii at an angle about equal to that occurring in *Dinotherium*. Thus, in a figure of a median longitudinal section of the skull of a young African Elephant given by Flower ('Osteology of the Mammalia,' ed. 2, p. 181, fig. 59), the somewhat convex occipital surface is inclined to the basis cranii at an angle of about 40 degrees—that is, at a more acute angle than in *Dinotherium*. In the skulls of two very young Indian Elephants this angle was about 50 degrees, and in Palæomastodon, in which in the adult the spongy bone is relatively little developed, the angle is only about 35–40 degrees in the middle line. Thus it appears that the forward slope of the occiput relatively to the basis cranii is not really greater in *Dinotherium* than in the later Proboscidea, but only appears so because, when the palate and tooth series in *Dinotherium* is placed horizontally, the basis cranii slopes steeply downwards instead of being nearly horizontal.

In *Dinotherium* no development of cellular bone seems to have taken place, the necessary surface for the attachment of the muscles supporting the heavy head being in this case supplied by the great widening of the occipital surface, which is carried out laterally on to the lateral extensions of the squamosals (*a.s.*). The pit for the nuchal ligament (*n.l.*) is both wide and deep: behind it the occiput is convex from before backwards, while at the sides it is gently convex in all directions. Anteriorly the occiput is bounded by the transverse portion of the lambdoidal crest (*l.c.*), which is slightly convex forwards: in front of this the parieto-frontal surface makes an angle of about 140 degrees with the occiput. Laterally the lambdoidal crest reaches the upper border of the temporal fossa at about its middle point, and thence is continued downwards and backwards along its border to the lateral processes of the squamosal. The lateral portion of the occiput thus bounded, projects far over the enormous temporal fossa, forming a kind of roof to its posterior portion. The fronto-parietal region of the roof is short from before backwards and in its middle portion is flat or slightly concave. It first narrows a little, and then widens out and slopes down towards the post-orbital (*p.orb.*) processes, which are presumably borne by the frontals though no sutures are visible. A little in front of the level of the post-orbital processes the fronto-parietal region of the roof is bounded by a thickened border, which is concave forwards and forms the upper edge of the remarkably wide nasal opening (*ex.n.*). There is no trace of the nasal bones; they may have been lost, but in any case do not seem to have formed any median projection over the nasal opening. The maxilla (*mx.*), which formed the sides of the nasal opening at least in part, is a very massive and greatly developed bone. Externally to its tooth-bearing and palatal region it is produced laterally into a shelf of bone the hinder border of which is opposite the hinder lobe of the first molar. Posteriorly it forms the floor of the orbit, and no

Text-figure 2.

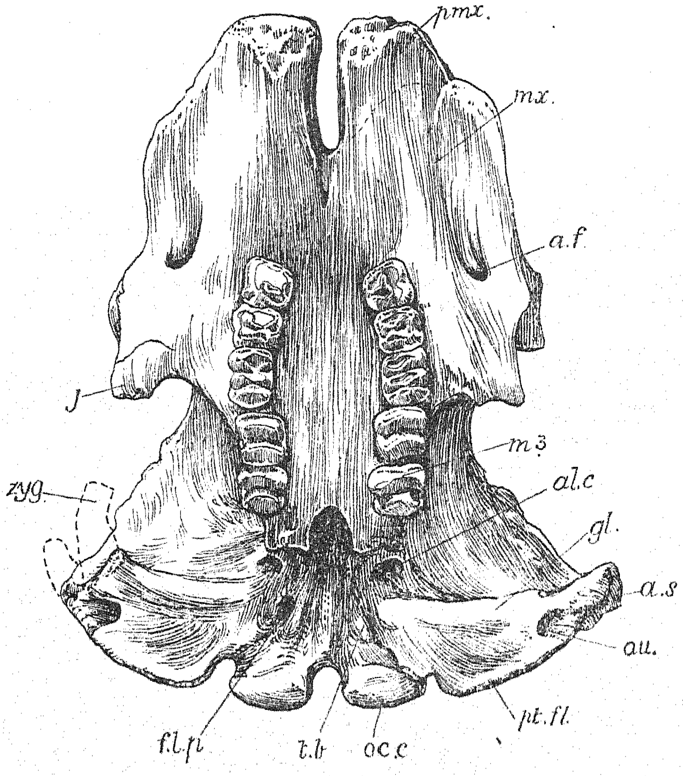


Skull of *Dinotherium giganteum*.
From above: about $\frac{1}{8}$ nat. size.

a.s., outer angle of squamosal; *ex.n.*, external nares; *jug.*, jugal; *l.c.*, lambdoidal crest; *n.f.*, nuchal fossa; *o.c.*, occipital condyles; *oc.s.*, occipital surface; *p.orb.*, postorbital process of frontal; *pt.fl.*, post-tympanic flange; *r.*, ridge from outer angle of squamosal.

doubt joined the jugal, on which the lower post-orbital process is borne. In front of the orbit the maxilla forms a great mass of bone, terminating laterally in a rugose somewhat concave surface for the attachment of a muscle (*m.s.*), probably the maxillolabialis superior. The lachrymal bone perhaps took part in the formation of this pre-orbital mass, but its limits cannot be determined. The very large antorbital foramen (*a.f.*) opens on the lower surface of the maxilla, about mid-way between its prominent pre-orbital boss and the premolar teeth. The point of union of the maxillæ with the premaxillæ is probably marked by the sudden narrowing of the snout about 40 centimetres in front of the orbit. The suture between the two bones can be traced for a short distance on the palatal surface.

Text-figure 3.



Skull of *Dinotherium giganteum*.
From below: about $\frac{1}{13}$ nat. size.

a.f., antorbital foramen; *al.c.*, posterior opening of alisphenoid canal; *a.s.*, outer angle of squamosal; *au.*, external auditory meatus; *f.l.p.*, ? foramen lacerum posterius; *j.*, jugal; *gl.*, glenoid surface for mandible; *m.* 3, third molar; *mx.*, maxilla: *oc.c.*, occipital condyles; *pmx.*, premaxilla; *pt.fl.*, post-tympanic flange; *t.b.*, ? tympanic bulla; *zyg.*, zygomatic process of the squamosal.

The premaxillæ (*pmx.*), though narrower than the maxillæ, are still very massive and widely expanded. Their upper surface is concave from side to side, the lower convex in the same direction. In the mid-ventral line they are separated in the actual skull by a cleft, probably the result of distortion through crushing: in the cast, which seems to have been made before the skull had been broken, there is only a deep groove. From the posterior angles of this groove a pair of ridges run back on the palatal surface to the anterior end of the tooth series.

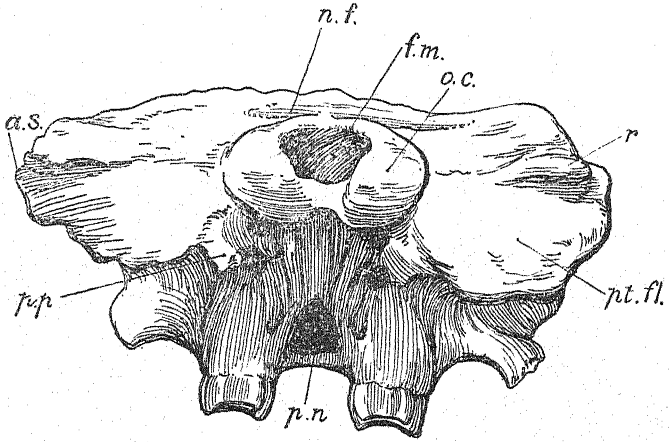
The anterior ends of the premaxillæ are thickened, and terminate in a nearly flat surface in which there are some irregular asymmetrically arranged pits but no real trace of any incisor alveoli, though it seems not unlikely that incisors will be found to have been present in the young animal. The anterior portion of the skull in front of the tooth series is curved downwards, its palatal surface approximately following the curve of the downturned mandibular symphysis.

The structure of the basal region of the skull is not very clear, probably in consequence of the crushing and fracturing it has undergone. On either side of the basioccipital there is a fairly well-developed auditory bulla (*t.b.*). External to this is a strong crest of bone, terminating posteriorly at the process described above as the paroccipital (*p.p.*). Anteriorly it runs inwards to the sides of the basisphenoid. This crest, which seems—at least in front—to be formed by the pterygoid, turns downwards anteriorly, and forms the border of the narrow opening of the posterior nares (*p.n.*): ventrally it terminates just behind the tooth series in a boss of bone which forms the posterior angle of the hard palate. Dorsal to this boss there is a deep fossa, presumably in the palatine, passing upwards to the hinder opening of the alisphenoid canal (*al.c.*). Behind and a little to the outer side of this opening is the inner end of the extraordinarily elongated glenoid surface (*gl.*) for the mandible. This surface is very narrow from before backwards and gently convex in the same direction: posteriorly it is bounded by the depression separating it from the post-tympanic flange. Its outer end is immediately behind the base of the zygomatic process (*zyg.*) of the squamosal, and its anterior border, at least in its outer half, abuts on the temporal fossa. The auditory opening (*au.o.*) is opposite the outer border of the zygomatic process: the external auditory meatus is greatly elongated, and its floor is formed by the roof of the channel behind the glenoid surface. Above the auditory opening the massive lateral angle of the squamosal (*a.s.*) projects outwards some fourteen or fifteen centimetres. The structure of a bony labyrinth supposed to belong to *Dinotherium* has been described and figured by Claudius ("Das Gehorlabyrinth von *Dinotherium giganteum*," Palæontographica, vol. xiii. (1864–66) p. 65).

The opening of the optic foramen is indicated by a depression, from the upper edge of which a downwardly deflected ridge (*or.r.*) runs upwards and forwards across the side wall of the skull and terminates in front in the post-orbital process (*p.orb.*). Towards its anterior end it becomes very prominent, sharply delimiting the eye-socket above. This ridge seems to be very characteristic of the Proboscidea: it occurs in *Mœritherium* and probably in all the members of the group.

The skull of *Dinotherium* is, in many respects, one of the most remarkable known. Although fundamentally its characters are clearly Proboscidean, nevertheless it differs widely from the skulls of the other members of the group and, indeed, in some respects from that of any other mammal. In the true Elephants and Mastodons the peculiar form of the skull is mainly due to the enormous development of cellular bone in the occipital region, increasing the area available for the attachment of the muscles necessary for the support of the heavy trunk and tusks. In *Dinotherium*, although the upper tusks are wanting, the trunk, judging from the large size of the nasal opening, must have been enormous, and the weight of the head was further increased by the great deflected mandibular symphysis with its large tusks. In this case, however, the area for the attachment of the supporting muscles was supplied by the widening out of the occipital surface, which was further increased laterally by the extension outwards of the squamosals. Little or no cellular bone seems to have been developed, the occipital surface above the post-tympanic flanges being nearly flat except for the depression for the nuchal

Text-figure 4.



Skull of *Dinotherium giganteum*.
From behind: about $\frac{1}{13}$ nat. size.

a.s., outer angle of squamosal; *f.m.*, foramen magnum; *n.f.*, nuchal fossa; *o.c.*, occipital condyle; *p.n.*, posterior nares; *p.p.*, paroccipital process; *pt.fl.*, post-tympanic flange; *r.*, ridge from outer angle of squamosal.

ligament. This flattening of the occiput, combined with its forward inclination, must have made it possible for the animal to move its head up and down through a large arc, a movement perhaps connected with the use of the downwardly directed lower tusks. The great width of the proboscis, probably rendered possible by the absence of upper tusks, led to the widening out of the skull in the orbital region, producing the shelf-like projection of the maxillæ above noticed. The great width of the glenoid surface for the mandible is a peculiarity for which it is difficult to account, unless it is correlated with the general widening of this region of the skull.

The skeleton of *Dinotherium* is still very imperfectly known, but such bones as have been described show that the animal must have been quite Elephantine in structure and appearance except as to its head, the legs being pillar-like and the neck short. A femur probably associated with the skull above described measured 150 cm. in length. The numerous speculations as to the appearance and habits of *Dinotherium* have been summarized by de Blainville and Stefanescu in their works referred to above. Most writers seem to suppose that the animal was chiefly fluviatile and aquatic in its habits, but there appears to be no good reason for believing that it was more so than the Elephants.

The origin of *Dinotherium* is a question of much obscurity. The genus must have branched off from the main Proboscidean stem at a very early date, probably originating from an animal in much the same stage of evolution as *Mœritherium*, the teeth being still simply bilophodont. The premolar series is more highly modified than in *Mœritherium*, the series being reduced to pm. 3 and pm. 4, the latter being bilophodont like the posterior molars. This modification of the premolars, like the acquisition of the third ridge in m. 1 and the reduction of the heel of m. 3, may have arisen after the divergence from the main stock had taken place. It is interesting to note that the last lower milk molar of *Mœritherium* shows a strong tendency to trilophodonty, the posterior ridge being fairly distinct: in *Dinotherium* also this tooth is trilophodont. If, as seems almost certain, *Dinotherium* originated from some small comparatively generalized type, it is interesting to note how, after its separation from the main stock, the direction of evolution is almost the same as in the latter. Thus there was a general increase in stature, which, being accompanied by a shortening of the neck, necessitated, as in the Elephants and Mastodons, the development of an elongated snout; so that it may be regarded as certain that *Dinotherium* passed through a longirostrine stage comparable to that of which the beginning is seen in *Palæomastodon* and the culmination, so far as the elongation of the lower jaw is concerned, in *Tetrabelodon angustidens*. Subsequently the symphysis became somewhat shortened and was deflected, the lower incisors at the same time becoming enlarged. It is interesting to notice that a tendency to a similar type of modification of the mandible occurs in that group of Tetrabelodonts to which Professor Osborn gives the name Rhynchorostrinæ, the most extreme case being *T. dinotherioides*. This deflexion of the mandibular symphysis led to the development of the flexible free trunk, just as the shortening of the symphysis did in the main stem, but while in this the upper incisors tended to increase in size, in the Dinotheres they disappeared.

The dimensions of the skull above described (taken on the cast) are:—

	cm.
Length from occipital condyle to tip of premaxillæ.	121
Length from posterior border of palate to tip of premaxillæ	84
Width between outer angles of the squamosals ...	90
Width between outer borders of the zygomatic processes	74
Width between the openings of the ear	68
Length of glenoid surface from before backwards.	6·3
Width of glenoid surface from side to side	24
Width of the occipital condyles	31
Width of skull just in front of the ant-orbital foramen	57
Width of the anterior end of the premaxillæ	31
Length of molar-premolar series	47
Length of molar series	30·2

29. On the External Characters of some Species of Lutrinæ (Otters). By R. I. Pocock, F.R.S., F.Z.S.

[Received April 19, 1921: Read May 24, 1921.]

(Text-figures 19–21.)

CONTENTS.

	Page
The Rhinarium	535
The Facial Vibrissæ	537
The Ear	537
The Feet	539
The Anus and External Genitalia	542
The Genera of Otters of the Old World	542
The Descent of the Lutrinæ	544

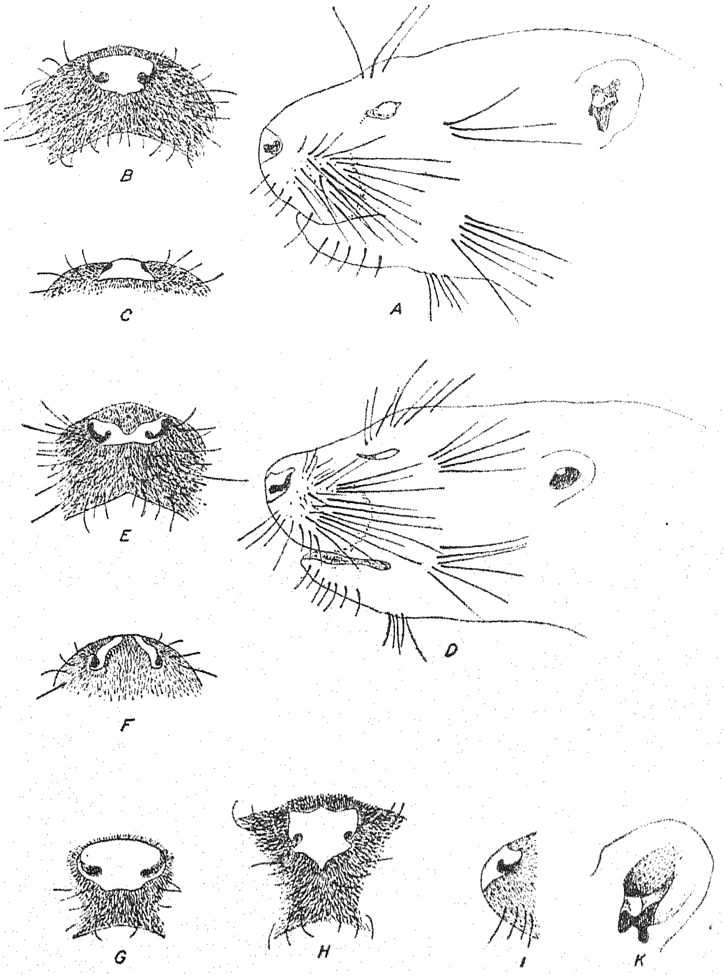
Since the different species of Otters are remarkably alike in general appearance, and the published notes on their external characters, to which Gray in particular paid great attention more than half a century ago, were taken apparently from dried skins, the following illustrated descriptions of the three species, *Lutra lutra*, *L. maculicollis*, and *L. cinerea*, exhibited during the past few years in the Zoological Gardens, supplemented by an examination of the softened skin of a stuffed example of *Aonyx capensis*, and followed by some general conclusions with regard to the systematic status of the species examined and the descent of the Lutrinæ, may prove of interest.

The Rhinarium.—The extent to which the rhinarium is covered with hair has frequently been used since Gray's time as one of the best external characters for distinguishing the species of Otters.

In *Lutra lutra* it is entirely naked and a little wider than long; but judging from descriptions is variable in shape. Gray, for example, described the lower edges as straight and the upper as "rather produced and angular." Blanford corroborates this, saying that the "upper edge is not straight but projects in the middle and is concave on each side, running up considerably to the hinder edge of the nostril." Miller, on the contrary, says the upper margin is "strongly convex at middle, the lower slightly so." In the specimen here figured the upper edge agrees precisely with Blanford's description, and the lower margin is angularly produced. The nostrils are widely separated and there is no philtrum, the upper lip being continuously hairy and about as deep as the height of the rhinarium. This species has a comparatively long muzzle, as shown by the skull, and the plane of the rhinarium is inclined upwards and forwards at an angle of about 60° or less.

In the Asiatic small-clawed Otter (*Lutra cinerea*), a short-

Text-figure 19.



A. Head of *Amblonyx cinerea*.
B. Rhinarium and upper lip of the same from the front.
C. Rhinarium of the same from above.
D. Head of *Hydrictis maculicollis*.
E. Rhinarium and lip of the same from the front.
F. Rhinarium of the same from above.
G. Rhinarium of *Aonyx capensis* from the front (skin dried and softened).
H. Rhinarium of *Lutra lutra* from the front.
I. Rhinarium of *Lutra lutra* from the side.
K. Ear of *Lutra lutra*.

All figures, except K, × ½.

jawed form, the plane of the rhinarium is almost vertical. Otherwise it closely resembles that of the European species, except that its upper edge is straight transversely between the posterior edges of the nostrils and its inferior edge less produced.

So far as it is possible to judge on the dried skin, the rhinarium of the African clawless Otter (*Aonyx capensis*) resembles that of the Indian form *L. cinerea*, which is often associated with it.

The other well-known African Otter (*Lutra maculicollis*) has a very different rhinarium, although as in *L. cinerea* its plane is vertical. It is very much reduced in size, being overgrown with hair to such an extent that little more than the edges of the nostrils are naked. The inferior border is quite straight and the infranarial portion on each side is shallow, while its upper edge is sinuously concave backwards, owing to the advancement of the hair in a curved line on each side from the posterior margin of the nostril to the middle line, where it nearly divides the rhinarium into two portions. From this it results that the middle of the rhinarium is less than one-fourth of the depth of the upper lip.

The Facial Vibrissæ.—The facial vibrissæ in Otters are, as a rule, exceedingly coarse and numerous as in most predatory aquatic mammals. Two points to be noted, however, are that the mystacials, as compared with those of normal terrestrial mammals, are relatively short, not longer that is to say than the genals, and that the genal tufts, especially the inferior, are exceptionally well developed, the vibrissæ being numerous and long. The material examined does not warrant the opinion that *Lutra lutra*, *L. cinerea*, and *L. maculicollis* differ in any way with respect to their vibrissæ; but the vibrissæ of *Aonyx capensis* are decidedly less stout and stiff, especially perhaps those forming the upper genal tuft *.

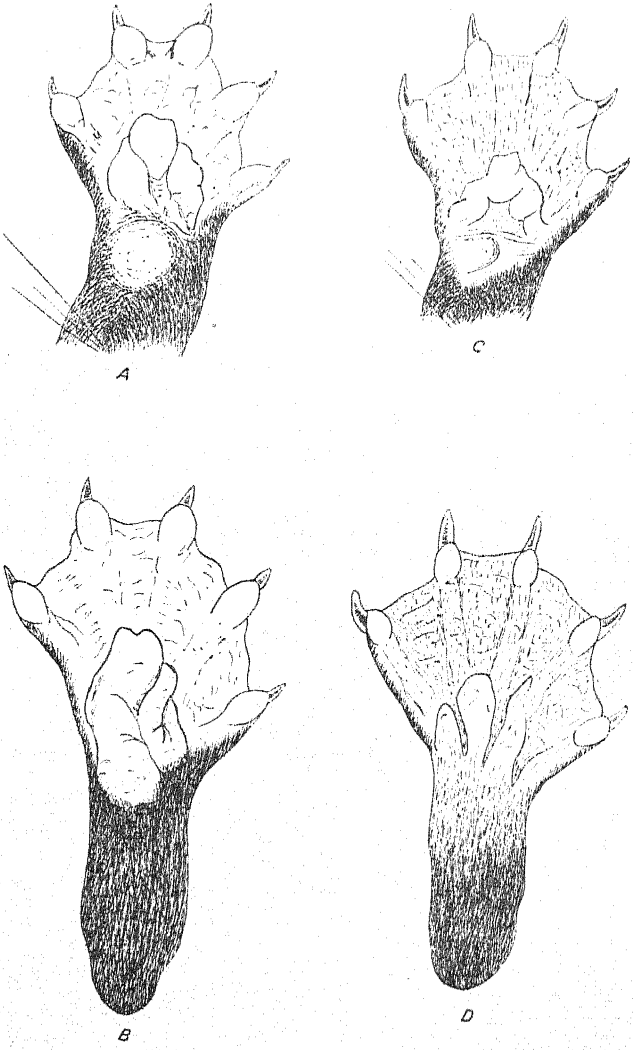
The Ear.—The external ear in Otters is always small and oval, and comparatively simple in structure, the bursa being absent. In the European species (*Lutra lutra*) the tragus and antitragus are tolerably well developed, with a well-marked notch between them, and just inside the antitragus there is a strong ridge-like thickening forming the posterior rim of the cavity. The supratragus is a shelf-like ridge with well-developed fleshy lobe.

In the Indian small-clawed Otter (*L. cinerea*) the ear is very like that of *L. lutra*, but relatively smaller, the cavity not extending so high above the supratragus; and the tragus and antitragus are inconspicuous. On the dried skin I could find nothing distinctive about the ear of *Aonyx capensis*. In *L. maculicollis* the ear is simpler than in *L. cinerea*. The inferior edge of the cavity shows no trace of a notch, the tragal and antitragal thickenings being altogether suppressed, and the supratragus is represented merely by a rounded tubercle corresponding to the fleshy lobe of this thickening seen in *L. lutra* and *cinerea*.

---

* Hinton (Ann. Mag. Nat. Hist. (9) vii. p. 195, 1921) has recently proposed the new generic name *Paraonyx* for two clawless Otters from the Congo which differ, amongst other things, from *Aonyx* in the complete suppression of the superciliary and upper genal tufts.

Text-figure 20.



A. Right fore foot of *Lutra lutra*.
B. Right hind foot of *Lutra lutra*.
C. Right fore foot of *Hydrictis maculicollis*.
D. Right hind foot of *Hydrictis maculicollis*.

The Feet *.—The feet of the Lutrinæ or Otters are so variable that it is hardly possible to mention a single character in which they differ from those of the other Mustelidæ collectively, except that the fore paw is always much smaller than the hind. In some cases the digits are less fully webbed than in any other genus of the family except *Lyncodon*; but in the typical forms the feet are more fully webbed because the digits are relatively longer and more widely separable, owing to the greater width and less emargination of the webs, especially of those joining the first and second, second and third, and fourth and fifth digits.

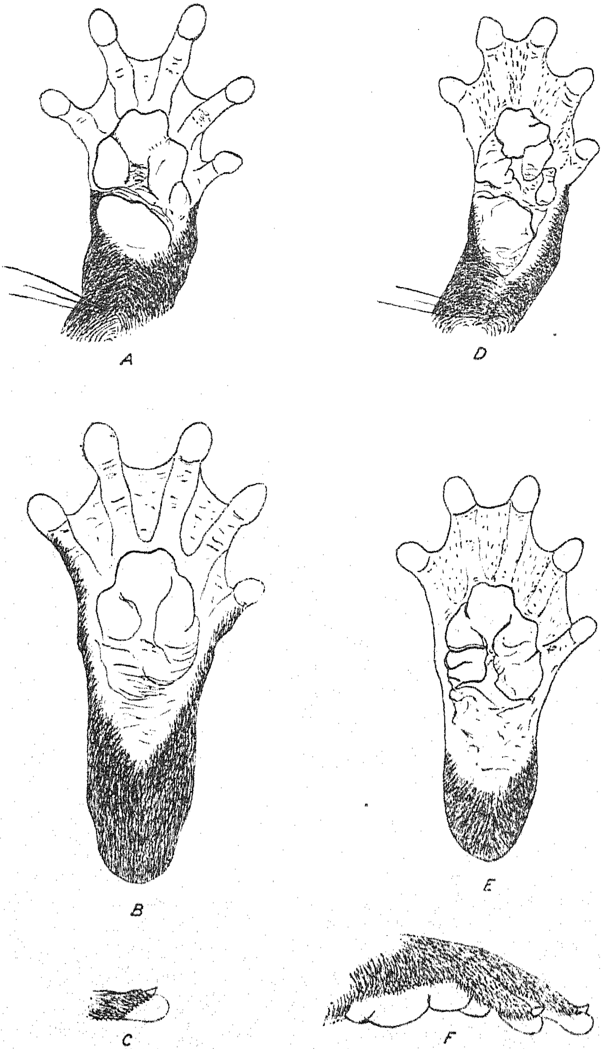
In *Lutra lutra*, for example, the third and fourth digits of the fore foot are not more widely separated nor more fully webbed than in *Charronia* or *Gulo*; but the webs between the fourth and fifth, and third and second, and second and first digits extend with a nearly straight edge between points near the middle of the margins of the digital pads. The claws are well developed and project well beyond the tips of the digital pads, and the sole of the foot is naked back to the proximal margin of the single large, sometimes nearly hemispherical, sometimes transversely elongated carpal pad. The radial or internal element of the carpal pad is not separately distinguishable. There is a short, naked area between the carpal and the plantar pad; and the main part of the latter is well developed but narrow, that is to say about as wide as long, and distinctly three-lobed; the two lateral lobes nearly meet behind the median, and the pollical element is small and indistinctly defined from the posterior end of the adjoining lobe. The hair of the wrist extends right down to the carpal pad. The hind foot is markedly larger than the fore foot owing to the greater elongation of the digits, which have consequently deeper and wider webs. The plantar pad is remarkably modified. Its median lobe is elongated and somewhat heart-shaped; the external lobe, defined by a deep groove, extends far back behind the median in contact throughout its length with the inner lobe, which is almost as long but has its free edge emarginate, the proximal or pollical element being large. The three main lobes just described are defined from each other by a Y-shaped groove. The hair of the metatarsus extends down to the proximal end of the plantar pad, and there is no trace of metatarsal pad.

In *Lutra maculicollis* the digits are relatively longer than in *L. lutra* and the webs are better developed, extending to the distal end of the digital pads on their inner sides. The plantar pad of the fore foot is more normally shaped, being considerably wider than long and four-lobed. The median lobe is not narrowed behind, the posterior ends of the main lateral lobes are widely separated, and the pollical lobe is clearly defined. The single ulnar carpal pad is much smaller than in *L. lutra*; and apart from the pads which are naked, the underside of the foot is covered with fine, short scattered hairs. The hind foot differs

---

* The carpal vibrissæ are present in all the specimens described.

Text-figure 21.



A. Right fore foot of *Aonyx capensis*.
B. Right hind foot of *Aonyx capensis*.
C. Tip of digit with minute claw of hind foot of same.
D. Right fore foot of *Amblonyx cinereus*.
E. Right hind foot of *Amblonyx cinereus*.
F. External aspect of fore foot of same, showing claws.

from that of *L. lutra* in similar respects, except that the plantar pad is very poorly defined, its three lobes gradually fading away into the scantily hairy area of the metatarsus at the proximal end of the digits. The median lobe is tolerably broad in front and tapering behind, the external lateral lobe is scarcely differentiated from the base of the fifth digit, the internal lateral is a mere thickened ridge of skin covering the base of the second digit, and there is no trace of the internal or hallucal lobe. The skin of the metatarsus close to the proximal ends of the digits and of the plantar pad is scantily hairy, like the lower side of the webs and digits; but above it is thickly haired as in *L. lutra*.

In *Lutra cinerea* the feet differ from those of *Lutra lutra* and *L. maculicollis* in being narrower owing to the shortness of the digits and the comparative shallowness and narrowness of the webs, which reach only to the proximal end of the digital pads, those joining the second and third, and fourth and fifth digits being decidedly emarginate, although not quite to the same extent as in cursorial and fossorial Mustelidæ. The claws, moreover, are very short, almost erect, and quite concealed when the feet are examined from below. The plantar pads also are better developed and more normal in shape, being longer than wide, subsymmetrical and four-lobed, the inner main lobe being prolonged by the pollical and hallucal elements. In the hind foot the outer main lobe is distinctly divided into an anterior and posterior portion by a transverse groove and almost in contact in the middle line with the internal lateral lobe. Above this pad the metatarsal area is mostly covered with naked wrinkled skin, the heel only being hairy. In the fore foot the carpal pad is relatively as large as in *L. lutra*, but it is defined above by a naked strip of skin over which the hair of the wrist does not extend. The lower sides of the webs and the grooves between the pads are beset with small hairs, but they are shorter and fewer than in *L. maculicollis*.

In *Aonyx capensis* *, the African clawless Otter, the hind foot is very like that of *L. cinerea* in the development of the digits and webs; but the hair on the metatarsal area extends farther towards the plantar pad. The fore foot also is tolerably similar to that of *L. cinerea* apart from the great difference that the webs between the digits reach only to the distal end of the first phalange, the ends of the digits being free. This terminal freedom of the digits from webbing is not found in any of the cursorial or fossorial Mustelidæ. A further peculiarity of this Otter is the suppression of the claws on the fore foot and on the first, second, and fifth digits of the hind foot. On the third and fourth digits of the hind foot they are merely retained as small flattish nails.

---

* I am greatly indebted to Mr. Fitzsimons, of the Port Elizabeth Museum, for very kindly sending me at my special request an example of this Otter from the collection under his charge. It was a mounted specimen, and the method of preservation made it impossible for me to ascertain the precise shape of the plantar and carpal pads.

A further stage in the disappearance of the webs is shown in *Paraonyx*, which is described by Hinton as having unwebbed digits on the fore foot and the digits of the hind foot webbed to the base of the second phalange, apparently as in the fore foot of *Aonyx*.

Anus and External Genitalia.—About the anus and external genitalia there is very little to be said, since they closely resemble those of such typical Mustelidæ as *Martes* in having the anus encircled and the perinæum covered with hair and the two normal anal glands present, with the scent of the secretion comparatively inoffensive. The penis of *Lutra lutra* is moderately long, and is supported by a stout, nearly straight baculum* about 60 mm. long, convex above, flatter and sometimes faintly grooved below, and gradually narrowed from the base up to the apex, where it expands into two short, deeply cleft, thick condyle-like branches, curved downwards. The branches are not alike, the right being a little thinner and less curved than the left. The urethra runs along the underside of the baculum, which is invested in soft vascular distensible tissue, and opens in the middle line below, just behind the condyle-like thickenings of the baculum.

The baculum of *L. cinerea* is very like that of *L. lutra*, but is of more even width throughout and the two terminal branches are not curved downwards.

The Genera of Otters of the Old World.

Apart from the incidental mention of *Paraonyx*, the Otters discussed in the foregoing pages have been referred to the two genera, *Lutra* and *Aonyx*. But if the nomenclature of this group is to be brought into line with that of other groups of Mammals, as the publication of *Paraonyx* seems to demand, it is certain that several generic and subgeneric terms long ago proposed but never as yet adopted will have to be restored to use. I have neither the material nor the time to go into the question beyond the limits of the species exhibited in the Zoological Gardens, of which skulls or skins, or both, are in the Society's possession.

Otters unfortunately, although so widely distributed, are very seldom in the live animal market, and it does not appear that more than the following species have been exhibited in the Gardens:—*Lutra lutra*, *L. barang* (entered as *nair*), *L. cinerea*, *L. maculicollis*, and *L. platensis*.

Each of the four exotic species has been severed from *Lutra*, and received a generic or subgeneric name. About *platensis*, named *Nutria* by Gray, I have nothing to say, the specimen having been sent unexamined to the British Museum. The Oriental species determined by Thomas as *barang* was referred by Gray to the subgenus *Lutrogale* under the name *monticola*. I have no personal knowledge of the external characters; but the skull appears to me to differ from that of *Lutra* in characters which by the modern standard must be regarded as of generic value. It is much higher; the much larger orbit is thrust so far forwards that its anterior rim is above the front edge of *pm.* 3, thus greatly reducing the length of the muzzle, lengthening the floor of the orbit, bringing the frontal postorbital process over the middle of the upper carnassial, and lengthening the area of the cranium between those processes and the "waist." Added to this, the anterior nares are much less sloped, the infraorbital foramen is almost concealed in profile view by its upper bar, and the teeth are out of all proportion larger, etc.

---

* Described by Blainville, Pohl, and other authors.

The long-clawed African Otter (*maculicollis*), the type of Gray's genus *Hydrogale*, differs from typical *Lutra* in the reduction of the rhinarium and the simplification of the ear; in the relatively large, more fully webbed and hairy-soled feet with reduced plantar pads; and in many cranial characters, especially the shortness of the muzzle, length of the orbital floor, and the generally immature aspect of the skull owing to the feeble development of constrictions, crests, and prominences.

Since the sum of the differences appear to me to be of generic value, I propose the name *Hydrictis* to replace Gray's twice preoccupied name *Hydrogale*.

In defence of the adoption of the name *Aonyx* for the African small-clawed Otter I need say nothing, since the genus appears to be admitted as valid.

The Oriental small-clawed Otter (*cinerea*) was named *Amblonyx* by Rafinesque in 1832. By modern writers it has been referred either to *Aonyx* or to *Lutra*, despite its differences from both. It resembles *Lutra* in the rhinarium, facial vibrissæ, and the ear, but differs in the structure of the feet, which are narrower owing to the shorter digits being joined by narrower webs, especially between the second and third and fourth and fifth digits, none of the webs extending beyond the proximal ends of the digital pads. The claws also are short and nearly erect or sometimes, according to Blanford, absent *; and only the calcaneal area of the hind foot is hairy. The skull also is very different from that of *Lutra*, and much resembles that of *Lutrogale barang* in the character of the muzzle and the size of the teeth, but is altogether much shorter from the frontal postorbital processes and the molars back to the occipital crest and condyles; the interorbital region is wider, the waist much shorter, and the orbital floor less extensive owing to the shortening of the tooth row.

In external characters *Amblonyx* differs from *Aonyx*, at all events, in the extension of the webbing of the fore feet to the digital pads and in the normal coarseness of the facial vibrissæ.

---

* The abbreviation of the claws of the front foot is accompanied in this Otter by extreme delicacy of the sense of touch in this extremity. I have seen one of these animals manipulating and playing with a marble in a manner recalling that of a conjuror juggling with a cricket-ball.

Thus four genera of Otters occur in Africa: *Lutra lutra*, north of the Sahara, *Hydrogale maculicollis* and *Aonyx capensis*, south of the Sahara, and *Paraonyx congicus*, etc., in the Congo area; and three in India, where they seem to be widely distributed: *Lutra lutra* or allied species; *Lutrogale barang*; and *Amblonyx cinerea*[*].

Omitting *Lutrogale barang*, whose external characters are only known to me from descriptions which supply no evidence of difference from *Lutra lutra*, these Otters may be distinguished as follows:—

- *a.* Fore feet with digits unwebbed; hind feet webbed to proximal end of second phalange; superciliary and upper genal vibrissæ suppressed (Hinton) .... *Paraonyx.*
- *a′.* Fore feet with digits at least half-webbed; hind feet webbed at least to proximal end of third phalange; superciliary and upper genal vibrissæ retained.
  - *b.* Fore feet webbed to proximal end of second phalange; facial vibrissæ comparatively slender and soft .... *Aonyx.*
  - *b′.* Fore feet webbed at least to proximal end of third phalange; facial vibrissæ comparatively stout and stiff.
    - *c.* Claws small or vestigial; digits short, webs narrow, reaching to proximal end of digital pads; hairs on metatarsus restricted to calcaneum; skull short, especially behind zygomatic arches. *Amblonyx.*
    - *c′.* Claws long, digits longer, webs wider, reaching at least half-way along digital pads; metatarsus hairy to plantar pad; skull long behind zygomatic arch.
      - *d.* Digits longer, more fully webbed, plantar pads poorly developed, especially on hind foot, carpal pad small, webs hairy below; rhinarium nearly covered with hair; ear simplified; skull with muzzle and mesopterygoid fossa short .... *Hydrictis.*
      - *d′.* Digits short, less fully webbed, plantar pads well developed, carpal pad large, webs naked below; rhinarium naked; ear with well-developed tragus, antitragus, and supratragus; skull with muzzle and mesopterygoid fossa long... *Lutra.*

The Descent of the Lutrinæ.

So far as I am aware, Miller is the only author who has attempted to affiliate the Lutrinæ definitely with one of the other subfamilies of Mustelidæ. This is embodied in the suggestion that they "appear to be essentially badgers modified for semi-aquatic life." Even granting the widest possible meaning to the word "badgers," I am quite unable to agree with this view. Miller, I think, placed too much reliance upon the teeth; but it does not appear to me that the teeth of *Lutra lutra*, perhaps the least modified of all the Otters, are more like those of *Meles* than of *Martes*. Again, in the Otters the shape of the skull, with its flat or slightly arched crown, its short muzzle, long back, and forwardly set posterior palatine foramina, forcibly recalls that of *Mustela* or *Grison*, and is quite unlike that of *Meles*, or indeed of any of the genera usually referred to the Melinæ, in all of which the skull has a long jaw and short back and, except in the

---

[*] I have not examined the type of Gray's genus *Barangia*, namely *sumatrana*, which is, I believe, the only other admitted species of Old World Otter.

Skunks, the palatine foramina in question placed on the maxillo-palatine suture.

Both *Mustela* and *Grison* are predatory terrestrial forms; and on *à priori* grounds it seems to be much more probable that the Otters are the descendants, modified for aquatic life, of some group of active, predatory terrestrial Mustelidæ than of comparatively inactive, specialized diggers like the Badgers. This view is supported by the long, slender, flexible body, the long tail, the broadly webbed, well spread digits, small claws and small front paws. These characters are found associated only in the genera currently referred to the Mustelinæ, but not in any of the so-called Melinæ, which have a short thick body, short tail, closely tied toes, powerful claws, especially on the fore feet, and the latter are larger than the hind feet.

Another point worth considering is the presence in a few unrelated species—i.e. *Lutra canadensis*, according to Gray, and in *Hydrictis maculicollis* and *Amblonyx cinerea*—of hairs upon the lower side of the webs of the feet. It seems to me to be difficult to explain their occurrence on the hypothesis of the descent of the Otters from naked footed Meline burrowers. The hairs seem to be quite functionless, and they have all the appearance of harmless vestigial structures suggesting the descent of Otters from hairy-footed forms. And since the Martens, Wolverenes, and Weasels, in the broad sense of the word, are the only members of the Mustelidæ, apart from the Otters just mentioned, which have hair upon the webs below, these hairs may be regarded as an additional item of evidence pointing to those active predatory Mustelidæ as standing nearest to the extinct ancestors of the Otters.

It is not of course suggested that the Otters are the descendants of any of the Martens or Weasels known to us, but that they are an offshoot from that line of descent; and I visualize their ancestor as an active terrestrial, predatory Mustelid with a well-developed tail and feet with the longish digits provided with short, sharp claws and united by wide webs, hairy below but not so hairy as in *Martes* or *Mustela*, and with the pads probably as large as in *Charronia*, with the skull shaped like that of *Mustela* or *Grison*, the auditory bulla like that of *Martes* and also the dentition, except that the upper carnassial had a larger inner lobe such as is seen in *Grison*.

The enlargement of the hind feet as compared with the fore feet, the thickening of the facial vibrissæ, with the correlated expansion of the upper lip and enlargement of the suborbital foramen, the reduction and simplification of the ear, the texture of the fur, and the muscular development of the tail, are special adaptions to aquatic life. Similarly, the enlargement of the back teeth, recalling in a measure that of the Melinæ, may be looked upon as an adaptation for breaking up fish-bones and rendering them harmless to swallow.

The explanation of the great difference in dentition between the Otters and the Seals may be explained in this way. Otters masticate their fish and require broad, flat-crowned teeth for the purpose. Seals swallow them entire, and the teeth are modified for catching and holding the slippery prey.

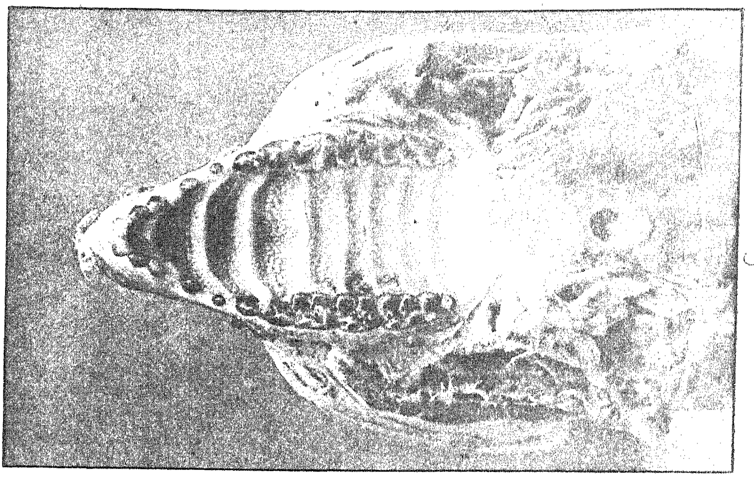
[NOTE.] After this paper was written, Mr. Thomas drew my attention to the elaborate monograph of the Lutrinæ published by Pohle in November 1920 (Arch. f. Naturg. 1919, pt. 9, pp. 1-247). So far as the species I have discussed are concerned, Pohle's systematic results, based upon skulls, teeth, and dried skins, differ in two points only from mine. While admitting the genera *Amblonyx* and *Aonyx*[*] as distinct from *Lutra*, he granted *Lutrogale barang* only subgeneric rank under *Lutra*, and dismissed *maculicollis* and two related species as "Die *maculicollis*-Gruppe" of *Lutra*[†]. Since the properly constituted subgenera and "groups" of species of one generation of workers almost invariably become the genera of the next, the fulfilment of their destiny in that respect by *Lutrogale* and the *maculicollis*-group may, I think, be confidently predicted.

I see no reason, therefore, for making any change in the text of this communication.

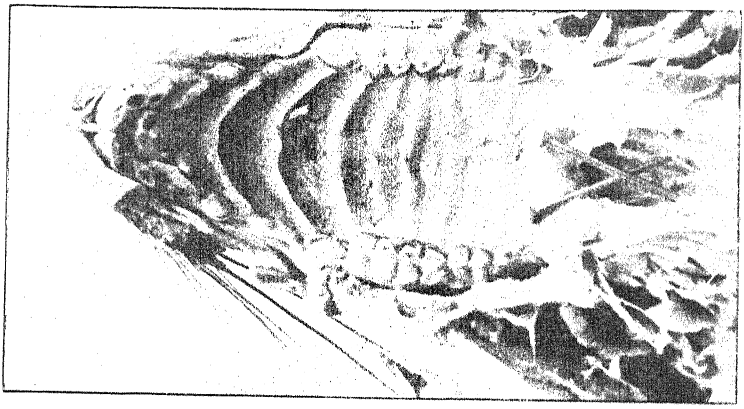
---

[*] Pohle missed *Paraonyx* although he had the description of *congica* before him and apparently plenty of material of the genus in the skins and skulls of the species he described as *Aonyx microdon*. This remark, however, is not intended as any disparagement of Pohle's work, which appears to me to be exceptionally good. In addition to the genera and species, it deals with geographical distribution, cranial changes with growth, milk-dentition, and so forth.

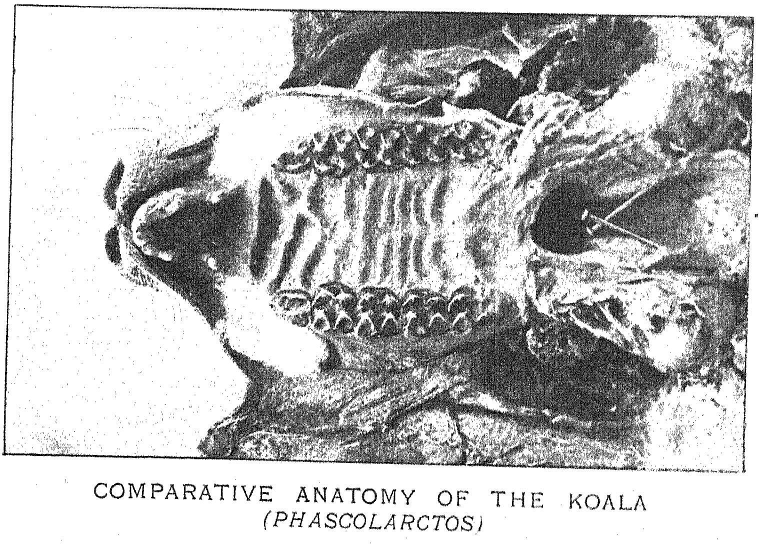
[†] Similarly, Pohle established "Die *Sumatrana*-Gruppe" [= *Barangia* Gray] and "Die *platensis*-Gruppe" for the American Otters *canadensis*, *annectens*, *enudris*, *platensis*, *provocax* and *felina*—a group for which the name *Lontra* Gray appears to be the oldest, with *Lataxina* and *Nutria* as synonyms.



C

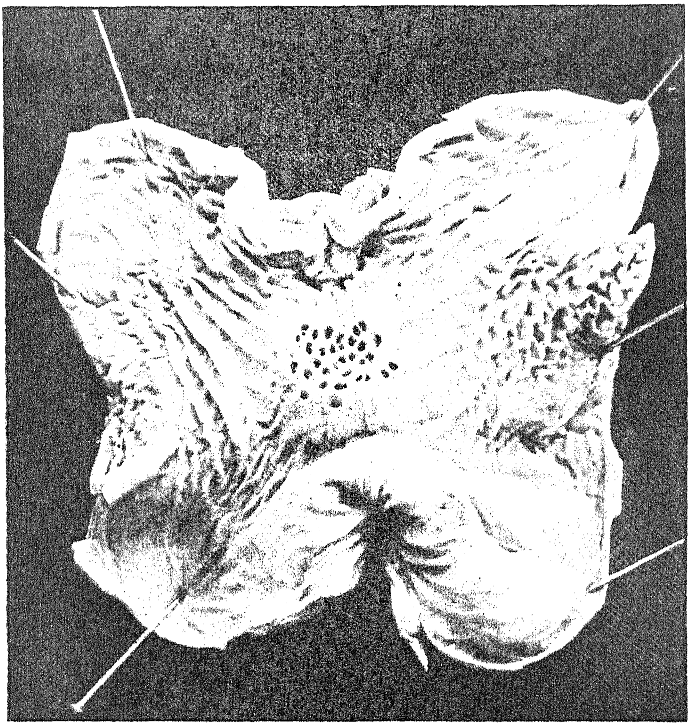


B

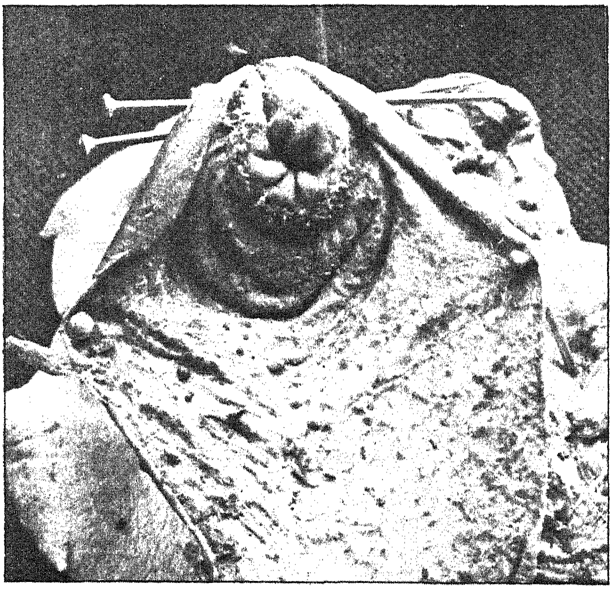


A

COMPARATIVE ANATOMY OF THE KOALA
(PHASCOLARCTOS)



A



B

COMPARATIVE ANATOMY OF THE KOALA
(PHASCOLARCTOS)

30. The Comparative Anatomy of the Koala (*Phascolarctos cinereus*) and Vulpine Phalanger (*Trichosurus vulpecula*). By Charles F. Sonntag, M.D., F.Z.S., Anatomist to the Society.

[Received May 7, 1921: Read June 7, 1921.]

(Plates V., VI.; Text-figures 53–63.)

The observations recorded here are based on the examination of an adult male *Trichosurus vulpecula* which died in the Society's Gardens, and a young female *Phascolarctos cinereus* which Mr. A. F. Richardson, of Hull, sent to us for examination after death.

The measurements of the Koala are as follows:—

	Centimetres.
Length from tip of nose to root of tail	50
,, of head	12·5
,, of tail	2·5
Greatest width of head	7·5
Length of fore limb (arm, 9·5; forearm, 13·5; manus, 4·5)	27·5
Length of hind limb (thigh, 11·5; leg, 12; pes, 5)	28·5

The external characters presented nothing new.

Sir Everard Home, who wrote the first account of the internal anatomy of the Koala, in 1808, described the character of the glandular patch of the lesser curvature of the stomach, and the prostate gland which resembles that of the Kangaroo; he also recorded the absence of the patella (**5**). Eighteen years later Dr. Robert Knox, of Edinburgh, described the long cæcum for the first time, and named the Koala the "Wombat of Flinders" in honour of its discoverer. He also criticised the writings of Home, Illiger, Cuvier, Desmarest, and De Blainville. Since then accounts of the anatomy of the entire animal have been written by Martin (**8**), Forbes (**4**), and Young (**13**), and individual organs have been described by Flower (**3**), Owen (**11**), Macalister (**7**), and Chalmers Mitchell (**9**). The histology of different parts has been described by Oppel (**10**) and Braus (**1**).

THE ANATOMY OF THE HEAD AND NECK.

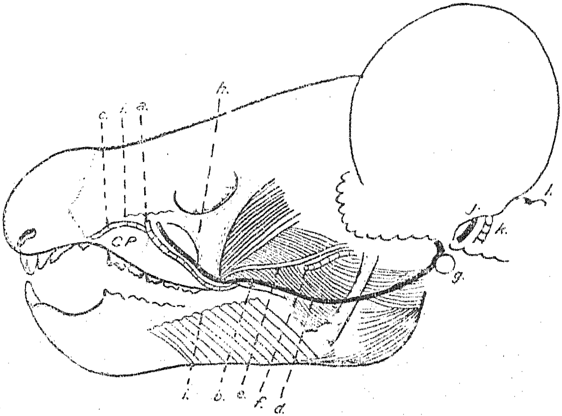
Phascolarctos cinereus.

When the skin of the head is removed it is seen how the platysma myoides, muscles of mastication, auricular muscles, and those round the orbit and mouth are strongly developed.

The *platysma myoides* arises posteriorly from a strong panniculus carnosus. It has a clearly-defined line of attachment to the lips, and some of its fibres fuse with those of the muscles of the angle of the mouth and orbit. It covers the anterior part of the masseter muscle and the facial vessels. It has been divided along the lines *i.i.* in text-fig. 53.

The *masseter muscle* (text-fig. 53) has been described by Macalister. It has a tendinous lower border (*b*), from under cover of which the *facial artery* (*a*) emerges and runs antero-superiorly; it gives off an external nasal branch (*c*) which runs along the antero-superior border of the cheek-pouch (CP). The masseter is crossed by the anterior facial vein (*d*), transverse facial artery (*f*), and Stensen's Duct (*e*).

Text-figure 53.



The side of the head of *Phascolarctos cinereus*.
j. k. posterior auricular vessels; *l.* parotid gland. Other letters in text.

Macalister has described the *attolens*, *attrahens*, and *retrahens* muscles which act on the large auricles.

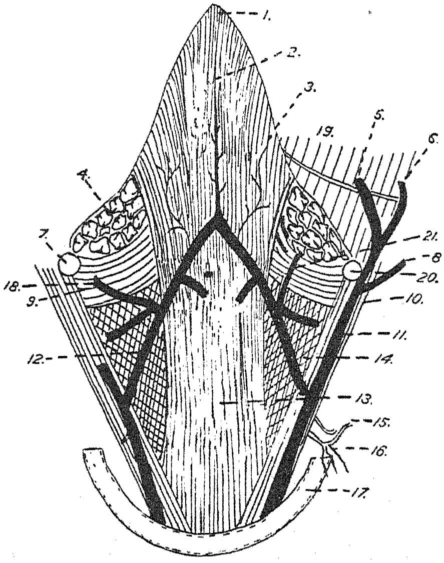
The *anterior facial vein* has the usual origin, course, relations, and branches. It unites with the posterior facial vein on the surface of the exoccipital process (*g*) to form the external jugular vein. No part of it is seen in the interramal space of the mandible, and the *vena transversa* (text-fig. 54, 12), which is long and V-shaped, connects the external jugular veins (11) instead of the anterior facials; it receives lingual, muscular (3, 18), sub-maxillary (21), and a single submental vein (2), but no *anterior jugular vein* connects it to the internal jugular vein.

The *Parotid Gland* is large, and forms a prominent mass in the face and neck. Running on its surface are the posterior auricular vessels.

The neck is divided, as usual, into mesial and lateral triangles by the sterno-mastoid muscle (text-fig. 54, 10), and these have the usual boundaries. The base of the lateral triangle is formed by the clavicle (17) as in all Marsupials except the Peramelidæ, which have no clavicles.

In the space between the mesial borders of the sternomastoids there is a thin muscular sheet formed by the mylo-hyoid (1) anteriorly, the digastrics (9) antero-laterally, and the sterno-hyoids (13) posteriorly; the sterno-hyoids have become separated from the hyoid bone in this specimen, but the whole sheet plays over it. Anterior to the digastrics are the submaxillary glands (4).

Text-figure 54.



The superficial anatomy of the neck of *Phascolarctos cinereus*.

5 and 6. anterior and posterior facial veins; 7, 20. exoccipital process; 8. posterior auricular vein; 11. external jugular vein; 16. supraclavicular nerves; 17. clavicles; 19. masseter. Other numbers in text.

The space between the sheet and the sterno-mastoids is bridged over by a triangular fascia (14) which covers the common carotid artery, vago-sympathetic nerve-trunk, and the nerve to the pretracheal muscles. It does not cover the internal jugular vein, which is under cover of the sterno-mastoid.

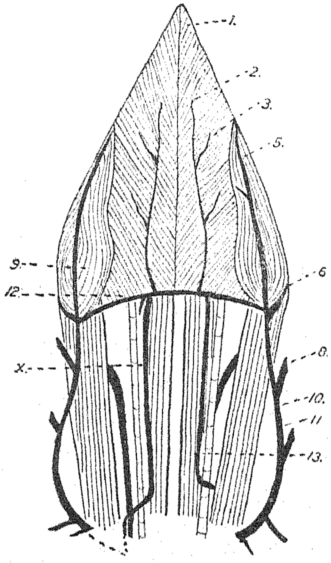
Trichosurus vulpecula (text-fig. 55).

The superficial anatomy differs from that of *Phascolarctos* in the following respects:—

1. The platysma is not so well developed. 2. The external nasal artery does not follow a cheek-pouch. 3. The auricular

muscles are not so powerful. 4. The vena transversa is horizontal, and runs between the anterior facial veins. It is connected to the internal jugular veins (*x*) and receives two submental veins; a small part of it loops into the interramal space. 5. The sterno-hyoid muscles are attached to the hyoid bone. 6. The superficial sheet between the sternomastoids of *Phascolarctos* is absent. Neither in *Phascolarctos* nor in *Trichosurus* does the vena transversa receive laryngeal veins.

Text-figure 55.



The superficial anatomy of the neck of *Trichosurus vulpecula*. Numbers as in previous figure.

The deep anatomy of the neck differs greatly in the two species:—

Phascolarctos cinereus.

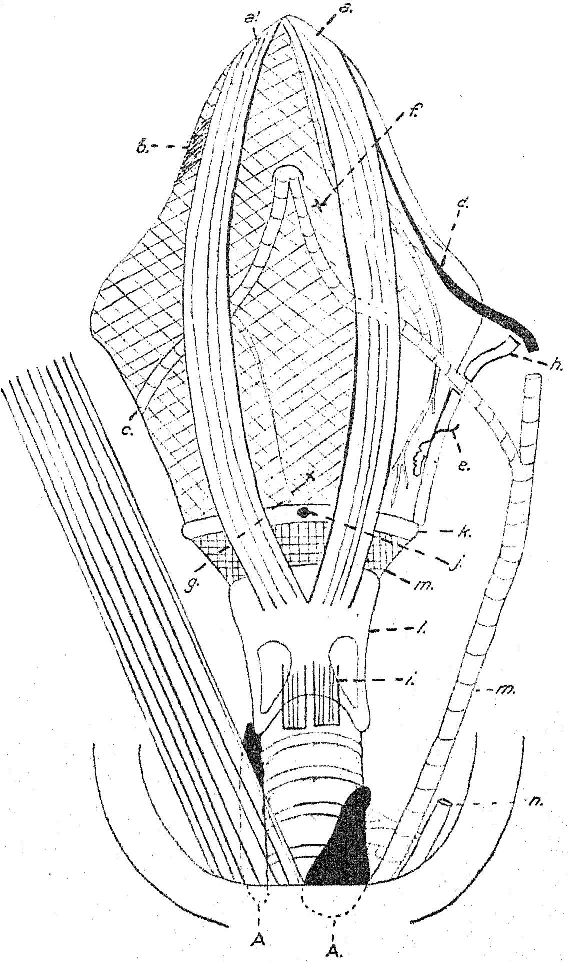
When the muscular sheet described above is removed the conditions shown in text-fig. 56 make their appearance.

The walls of the mouth (*f*) and pharynx (*g*) lie immediately under cover of the muscular sheet, and the following structures are seen to lie on their external surface:—

1. Two long, narrow strap-like genio-hyoid muscles (*a*, *a'*) running from the symphysis menti to be attached to the hyoid bone (*m*) and larynx (*l*). They cross the lingual arteries (*c*). 2. The lingual arteries. 3. The hypoglossal nerves (*d*). 4. The pharyngeal branches of the vagi (*e*), which are very tortuous.

A short interval separates the insertions of the genio-hyoid and sterno-thyroid muscles (*i*), which arise from the back of the sternum and third costal cartilages. At the posterior part of

Text-figure 56.



The deep anatomy of the neck of *Phascolarctos cinereus*.
j. level of opening of nasal tube into the pharynx; *k*. thyro-hyal capping the shaded basi-hyal (*m*). Other letters in text.

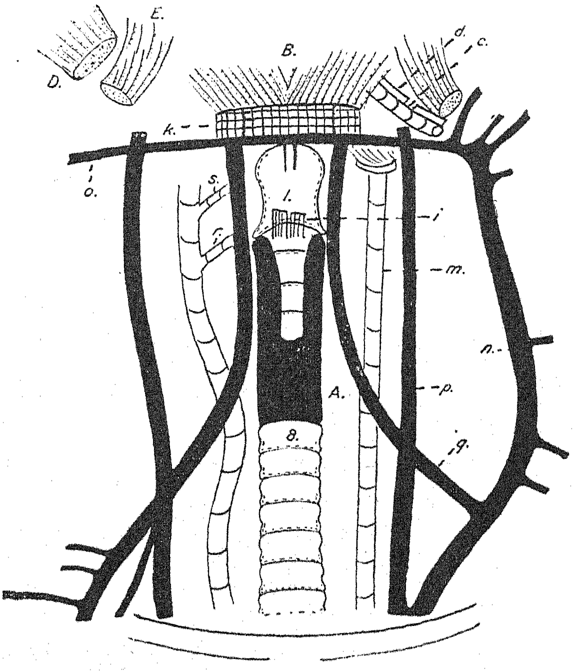
the neck the lateral lobes of the thyroid gland (A. A) project from under cover of the sterno-thyroids, and extend for a short distance dorsal to the clavicles.

Macalister (7) described the *styloid group of muscles* as follows:—"The styloid group form a single sheet, the hind fibres of which pass to the pharynx, the middle to the ceratohyal under the stylohyoid ligament; the anterior pass to the side of the tongue."

The *digastrics* have the usual attachment, and they are united by muscular fibres to other muscles around.

The *stylo-hyoid ligament* is loose (text-fig. 56, *h*). The genio-hyoids are connected to the digastrics by muscular slips (*b*).

Text-figure 57.



The deep anatomy of the neck of *Trichosurus vulpecula*.

D. sterno-mastoid; E. digastric; *k*. hyoid bone; *m*. common carotid artery; *n*. external jugular vein; *o*., vena transversa; *q*. anterior jugular vein; *r*. *s*. thyroid and laryngeal arteries. Other letters in text.

The *cervical lymphatic glands* form two groups. The first, consisting of a few large glands, is a little posterior to the prominent alisphenoid bullæ The small glands of the second group are around the great veins at the root of the neck.

The distance from the symphysis menti to the level of the angles of the mandible is 6 cm., from the angles of the mandible to the hyoid bone 1·2 cm., and from the hyoid bone to the sternum 6 cm.

Trichosurus vulpecula (text-fig. 57).

The deep anatomy of the neck differs from that of *Phascolarctos* in the following respects:—1. The walls of the mouth and pharynx are more deeply placed under muscles. 2. True hyoglossus muscles are present (B), so the lingual artery (*c*) and hypoglossal nerve (*d*) are more deeply placed. 3. The thyroid gland is applied to the posterior part of the larynx and is far anterior; it does not pass dorsal to the clavicles. 4. The alisphenoid bullæ are not so prominent. The exoccipital processes are not visible. 5. The external jugular vein is formed on the surface of the sternomastoid muscle.

THE RESPIRATORY ORGANS.

In *Phascolarctos* the epiglottis is broad and entire, with an emarginate apex, and each lung contains two lobes; Forbes (**4**) described two left and three right lobes. No azygos lobe is present. In *Trichosurus* the epiglottis is notched; the left lung has two lobes and the right one has four, of which one is azygos. The tracheal rings are wide, but deficient dorsally.

The nasal tube of *Phascolarctos* has no median dorsal ridge, and does not grip the larynx, whose epiglottis is so large that it could only be accommodated by considerable stretching of the orifice of the tube.

In *Trichosurus* the nasal tube has a median dorsal ridge, and it gripped the larynx firmly in my specimen.

Sir Everard Home states that the Koala utters a shrill yell when hungry or hunted, but Owen says that he never heard a note of any kind from the Phalangers.

THE MOUTH.

Phascolarctos cinereus.

The Vestibule.—Fleshy lips are connected to the gums by lax frenums, of which the upper is ·6 and the lower is 1·2 cm. long. The cheeks are attached to the gums opposite the canine tooth and posterior border of the premolar of the upper jaw on each side; between these lie the mouths of the cheek-pouches (Plate V., A) already described by Owen (**11**), Young (**13**), and Forbes (**4**).

Forbes states that "the mucosa of the cheeks is smooth throughout"; but in my specimen it is covered with rounded papillæ, which are all visible to the naked eye. They extend on to the fauces, and for a short distance along the outer walls of the cheek-pouches, but they are absent from the lips whose mucosa is quite smooth. They are not regularly arranged like the papillæ of the cheeks of the Ungulata.

The vestibule and cavum oris communicate through the diastema anteriorly, and behind the last pairs of molar teeth posteriorly; the former of these is wide and the latter narrow.

The Palate (Plate V., A).—The upper incisor and canine teeth surround a small area on which there are six small tubercles, but these do not cover prominences on the premaxillæ. Immediately behind these lies the first of the nine palatal ridges, which are most marked anteriorly. Forbes also described nine ridges, and Young recorded eight. Martin described eight furrows. The anterior ridges are transverse, and are complete or incomplete, but some of the posterior ridges are curved and bear small nodules on their anterior borders.

When the mucous membrane is removed the bony palate is seen to have a sinuous outline when viewed laterally (text-fig. 59, E).

The *soft palate* is long, smooth, and devoid of a uvula.

The *isthmus faucium* (text-fig. 59, *f*) is a circular orifice which admits the tip of the index finger, and the fauces form a septum without the tonsils, which lie far back in the pharynx at a distance of 6 cm. from the incisor teeth.

Trichosurus vulpecula (Plate V., B).

Cheek-pouches are absent, and the vestibule and mouth communicate as in the above. On the palatal area surrounded by the incisor and canine teeth, which form a more perfect arcade than in *Phascolarctos*, there is a median ridge and several small, hard papillæ.

The palatal ridges, of which there are six, are sharper than in *Phascolarctos*, and the anterior ones are convex forwards, with the free edges directed backwards. Between several of the ridges the mucosa is covered with papillæ.

The tonsils have the usual situation in the fauces.

Pseudochirus peregrinus (Plate V., C).

There are eight palatal ridges, most prominent anteriorly, and many papillæ crowd the mucosa between them. Cheek-pouches are absent.

THE TONGUE (text-fig. 58).

Martin (8) states that the tongue of *Phascolarctos* rises abruptly from a furrow surrounding its base, and the distance from its root to the epiglottis is $\frac{7}{8}$ of an inch. I found, however, that it is much farther removed, the distance being slightly more than $1\frac{3}{4}$ inches, and the mucosa of its dorsum is continuous with that of the ventral wall of the pharynx (text-fig. 59, A, *a*).

Measurements:—Total length 5·5 cm.; length of the oral part 5 cm.; length of the pharyngeal part ·5 cm.; greatest width 1·5 cm. The slightly spatulate narrow tongue does not narrow greatly from base to apex.

The Papillæ.—A single prominent *vallate papilla* (text-fig. 58, A) lies in the mid line; it is circular on plan and conical on elevation, with the base of the cone projecting beyond the well-marked fossa; the vallum is rough, granular, and not easily distinguished from the rough surface of the tongue. Martin, Owen, and Forbes each describe a specimen with one papilla.

The *fungiform papillæ* are small, and form a dorsal bounding zone on which they have the usual arrangement in clusters and rows; none are overlapped by the *conical papillæ*, which are small, pointed, and irregular in distribution. On the ventral papillary zone only conical papillæ are found.

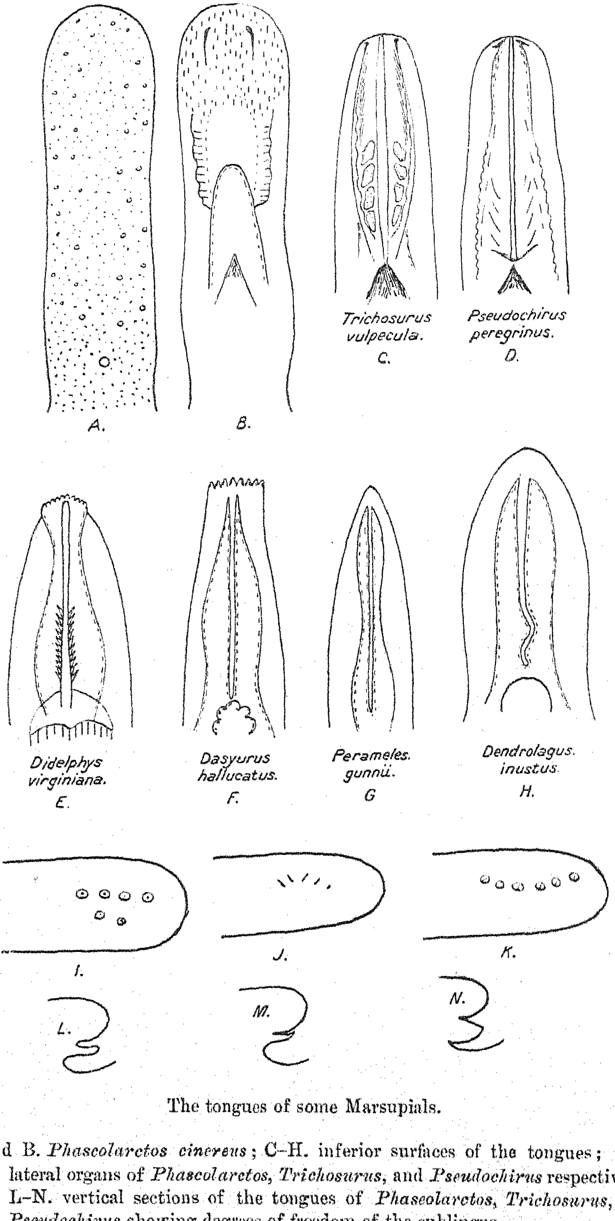
Although there are no *lateral organs* similar to those of the Primates, the posterior extremities of the corrugated lateral borders have circular nodules with well-marked central orifices (text-fig. 58, I); some of these are single and isolated, but others are in small chains. Poulton (**16**) has described similar bodies in *Halmaturus ualabatus*, *Macropus melanops*, and *Petrogale xanthops*, but points out that their arrangement varies; they may be irregular or arranged in curves. He draws attention to their appearances being similar to those of gland-ducts, and suggests that the lateral organs arise from glands; "this view," he states, "is confirmed by a study of minute structure."

No Apical Gland of Nuhn is present, but the glandular mass, as described and figured by Oppel (**10**), sends two long processes forward almost as far as the apex of the tongue. He believes that the Gland of Nuhn, which is present in the tongue of Man and the Orang-Outan, are pieces of the basal glandular mass which have become separated. Perhaps they have become separated off from a prolongation similar to those of the Koala and other Marsupials.

The *inferior surface* is wrinkled and fissured. In the mid line in front there is a well-marked rough area, bounded laterally by fissures. Posterior and lateral to the central area are crenated, transversely-furrowed *plicæ fimbriatæ* (text-fig. 58, B), which increase in width from before backwards.

Many Marsupialia have a sublingua which differs from that of the Lemuroidea in being firmly fixed by its apex to the under surface of the tongue. It varies in size in different species, but that of the Koala is the smallest; it has been reduced to the condition of plicæ fimbriatæ in the same way as the sublingua of the Lemuroidea gives way to the plicæ of the Simiidæ. A few illustrations of the degrees of development in the Marsupialia are shown in text-fig. 58, B–H. The sublingua also becomes softer as well as reduced in size, as in the Primates. Thus there is the complete horny sublingua as in *Lemur*, the softer and smaller sublingua as in *Tarsius*, and the plicæ fimbriatæ as in *Anthropopithecus*.

Text-figure 58.



The tongues of some Marsupials.

A. and B. *Phascolarctos cinereus*; C–H. inferior surfaces of the tongues; I–K. lateral organs of *Phascolarctos*, *Trichosurus*, and *Pseudochirus* respectively; L–N. vertical sections of the tongues of *Phascolarctos*, *Trichosurus*, and *Pseudochirus* showing degrees of freedom of the sublingua.

Trichosurus vulpecula.

Poulton (16) described the tongue under the old name of *Phalangista vulpina*, so I shall only mention the differences between it and that of *Phascolarctos*:—1. The epiglottis overlaps the base. 2. Three papillæ form a vallate triangle. 3. The lateral organs consist of fissures and laminæ. 4. The sublingua is a flat horny plate with a strong median ridge and a denticulated apex bound down to the under surface of the tongue (text-fig. 58, C). 5. The two forwardly-directed glandular processes are stouter and relatively shorter.

Pseudochirus peregrinus.

The parallel-sided tongue has the following *dimensions*:—Total length 4·2 cm.; length of the oral part 3·7 cm.; length of the pharyngeal part ·5 cm.; width between the lingual attachments of the palato-glossal folds ·4 cm.

The Papillæ.—Three circular *vallate papillæ* form an equilateral triangle with the apex behind; the basal papillæ are prominent, but the apical one is strongly retracted.

The *fungiform papillæ*, which are small and few in number, form a dorsal bounding zone, but they have no definite arrangement in transverse rows and clusters; they are surrounded by sharp *conical papillæ*, which form transverse rows almost up to the apex of the tongue. Only conical papillæ are present on the ventral bounding papillary zone.

No *orifices of ducts and glands* are seen on the base of the tongue.

The Lateral Organs (text-fig. 58, K).—On each lateral border of the tongue there is a row of circular elevations with central slit-like orifices, so they are not quite similar in appearance to those of *Phascolarctos*. The slits run upwards and backwards. Each organ consists of six areas. On the surrounding mucosa there are many nodules and papillæ.

The Sublingua (text-fig. 58, D).—The most pronounced feature of the tongue is the large, soft sublingua. It is firmly bound to the under surface of the apex, as in all Marsupialia in which it is complete, but its under surface is deeply fissured and separated by a deep gap from the tongue (text-fig. 58, D and N). Running backwards in the mid line is a strongly-developed median crest, which is bounded behind by a fissure.

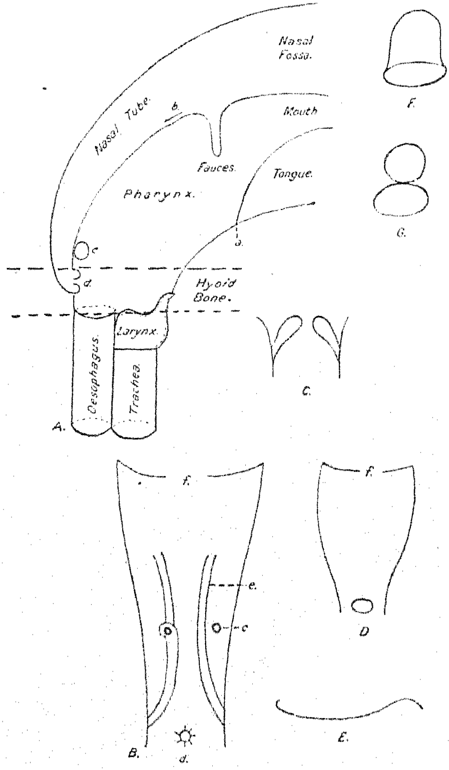
There are great differences, therefore, between the lateral organs, ventral surfaces, and vertical sections of the tongues of these three species, as seen in text-fig. 58, B–D and I–N. The essential differences between the sublinguæ of the Marsupialia and Primates lie in the apices—in the former the apex is fixed to, but in the latter it is free from, the under surface of the tongue.

THE PHARYNX.

Phascolarctos cinereus.

The distance from the fauces to the beginning of the œsophagus is 4·5 cm., and the greatest width of the pharynx, which narrows from before backwards, is 2·2 cm. The mucosa is smooth, and two ridges run along the sides of the mid-dorsal line (text-fig. 59, *e*).

Text-figure 59.



The pharynx of *Phascolarctos cinereus.*
Explanation of letters in text.

The *tonsils* (text-fig. 59, *c*) are small oval bodies in the dorso-lateral aspect of the pharynx, a little distance anterior to the hyoid bone. They appear as pits on the interior of the pharynx, and the right one is surrounded by a prominent ridge.

The *naso-pharynx.*—The nasal fossæ are prolonged backwards by a conical tube, which opens on the mid-dorsal wall of the pharynx by a small circular orifice guarded by two fleshy cushions (text-fig. 59, A *d* and C). It has no mesial dorsal ridge as in

Trichosurus and *Pseudochirus*. The opening lies within the hyoid ring about 5 mm. anterior to the beginning of the œsophagus, so the naso-pharynx is exceedingly small. This is a remnant of the condition present in the new-born animal. Owen (**11**) describes how the larynx is gripped by the nasal tube in the mammary fœtus of the Kangaroo, and the milk stream is divided by the larynx, which crosses the pharynx; he gives illustrations.

Sections through the head and neck at different levels show how the shape of the nasal tube alters from before backwards (text-fig. 59, F and G).

The *Eustachian Tubes* (text-fig. 59, *b*).—The lower orifices of the tubes are slit-like, and lie on the infero-lateral aspects of the nasal tube at a distance of 2·9 cm. posterior to the hard palate, and at a point about 1 cm. posterior to the fauces. In Plate V. pins are inserted into the inferior orifices of the Eustachian tubes.

Trichosurus vulpecula.

The pharynx differs from that of *Phascolarctos* as follows:—

1. The tonsils are in the fauces.
2. There is a ridge on the dorsal wall of the nasal tube, but none in the pharynx.
3. The larynx crosses the pharynx and enters the nasal tube.

The nasal tube of *Pseudochirus* has a median dorsal ridge (Plate V., C).

THE ŒSOPHAGUS.

Phascolarctos cinereus.

The *cervical part* (4·3 cm. long) is entirely concealed by the larynx and trachea, and its mucosa is smooth throughout. The *thoracic part* (7·8 cm. long) has small longitudinal folds on its inner surface. The *abdominal part* (1·8 cm.) is lined by mucosa thrown into prominent longitudinal folds. At the point where it emerges from the posterior surface of the liver it is in contact dorsally with the right suprarenal capsule.

Trichosurus vulpecula.

The œsophagus projects beyond the left border of the trachea in the neck, and it has a longer course (=3 cm.) in the abdomen than has that of *Phascolarctos*. It is not in contact with the right suprarenal capsule. In some examples its abdominal part is much shorter, however.

THE PERITONEUM.

Phascolarctos cinereus.

The *great omentum* is devoid of fat, but contains a well-marked arterial arcade formed by a branch of the splenic artery and a twig from the arterial ring round the pyloro-duodenal junction (text-fig. 60, B, a'). There is nothing new to record about its attachments.

The *lesser omentum* has a T-shaped attachment to liver and stomach (text-fig. 60, A, *a*). The horizontal limb lies along the lesser curvature, and the vertical limb runs back along the ventral surface of the stomach.

The great omentum of *Trichosurus vulpecula* is well laden with fat.

THE STOMACH.

Phascolarctos cinereus.

The observations recorded here are supplementary to the descriptions by Martin (**8**), Young (**13**), Forbes (**4**), Edelmann (**2**), Flower (**3**), and Home (**5**).

The long axis of the sac-like stomach, which lies in the epigastrium and left hypochondrium, runs posteriorly, ventrally, and to the right, and the well-marked fundus is directed forwards and to the left. Projecting from the greater curvature immediately below the pyloric cylinder is a sac whose walls are thinner than those of any other part of the stomach.

Relations :—

Anteriorly—liver and right suprarenal capsule.

Posteriorly—spleen, intestines, solar plexus, left kidney, and suprarenal capsule.

Right—duodenum, gall-bladder.

Left and ventral—abdominal parietes.

Dorsal—crura of the diaphragm, aorta, pancreas, right kidney, inferior vena cava.

Measurements :—

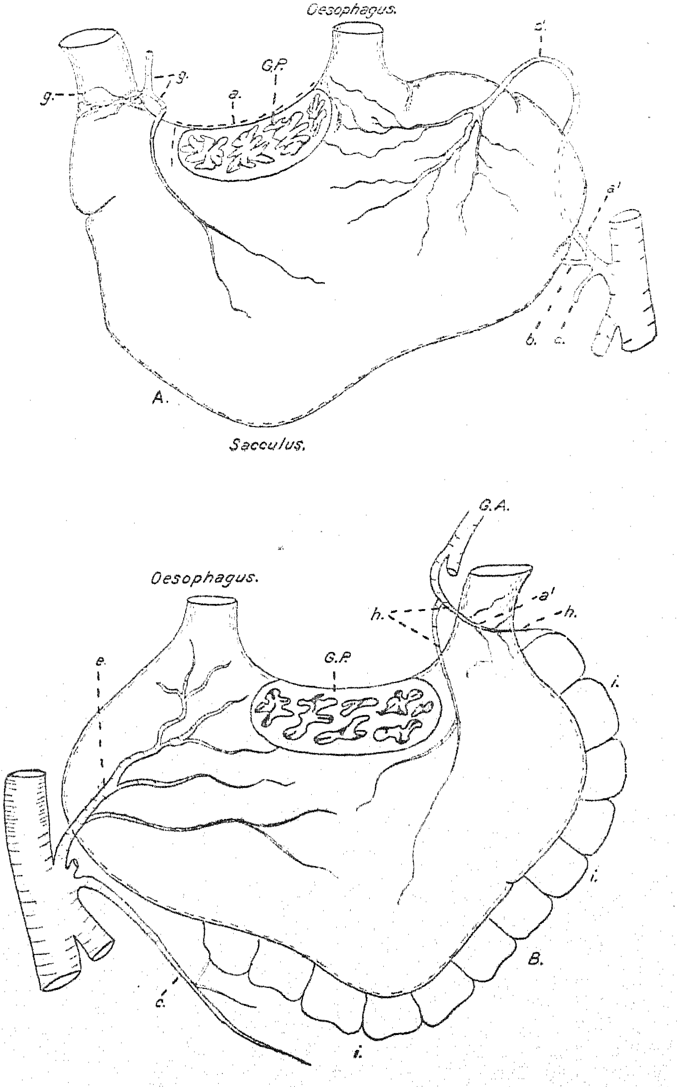
Total length	7 cm.
Length of fundus	2·2 ,,
Width between curvatures	3·7 ,,
Lesser curvature	2·2 ,,
Length of pyloric tube	1·6 ,,

Arteries (text-fig. 60).—The stomach receives its blood supply from the three branches—gastric (a'), hepatic (*b*), and splenic (*c*) —of the cœliac division of the cœliaco-mesenteric artery (see page 570), and each vessel is accompanied by fine nerves derived from the vagus and solar plexus (text-fig. 60, A).

The gastric artery divides into a large ventral branch (*d*) and two dorsal branches (*e*)—large and small. The former, after a straight course towards the stomach, breaks up into many tortuous vessels ramifying over the fundus, and some can be traced into the left side of the gland-patch. The latter make a similar vascular arrangement on the dorsal aspect of the fundus, and supply the patch as well.

The hepatic artery gives off a large gastric branch (G. A.) which divides into four—two dorsal (*g. g*) and two ventral—branches (*h. h*). Each pair supplies one surface of the stomach,

Text-figure 60.



The ventral (A) and dorsal (B) surfaces of the stomach of *Phascolarctos cinereus* with arteries.

and forms half of a vascular ring encircling the pyloro-duodenal junction. They supply the gastric wall and gland-patch. The pyloro-duodenal ring communicates with the mesenteric arteries, and a twig forms a long arcade (*iii*) in the great omentum with a branch of the splenic artery; this arch gives off vasa brevia, which enter the stomach-wall vertically (text-fig. 60, B).

There is no continuous vessel or arcade on the lesser curvature, for the gland-patch interrupts it.

The *veins* enter the portal and splenic veins.

The *gastric nerves* (text-fig. 63, V.G.P.) form a complex plexus on the left side of the gland-patch, and are intermingled with branches of the gastric artery, and fine nerves reach the stomach along branches of the hepatic artery. They will be described later along with the solar plexus and vagus nerves. The nerves reach the interior along the course of the arteries.

The *interior of the stomach* (Plate VI., A) was briefly described by Martin (8). Apart from the enumeration of the orifices of the gland-patch by several authors, no other description of the interior has been published.

The long axis of the oval gland-patch, which lies along the lesser curvature of the stomach, is 2 cm. long, and the width is 1·7 cm. Its inner surface has thirty orifices of different sizes, arranged in rows at right angles to the long axis of the patch. In addition to these the lens reveals how the surface of the patch is finely-pitted.

The remainder of the inner surface is traversed by rugæ radiating from the edges of the gland-patch like the spokes of a wheel. Those running towards the lower end of the œsophagus are short and Y-shaped; those passing into the fundus and body of the stomach are at first straight but undulating later; none are present in the sacculus on the greater curvature; and those passing to the pylorus are few in number, but stronger than in other parts.

The musculature of the pylorus thins out on the walls of the sacculus, and that of the œsophagus thins out on the fundus and lesser curvature.

The gastric contents consisted of a viscid creamy chyme, and they resembled the contents of the stomachs of two Langurs which I examined. In the Sloth, on the other hand, as I showed in a previous paper, the stomach contained many hard, almost entire leaves.

Special gastric glandular apparatus is also present in the Wombat, Beaver, Dormouse, Manatee, and Dugong. It was also present in the now exterminated Steller's Sea-Cow (*Rhytina stelleri*). Knox thought that the apparatus in the Sirenia was an electric organ, and traced the two vagus nerves into it.

The pylorus projects into the duodenum (Plate VI., B), as in Man. The human form has been likened to the projection of the cervix uteri into the vagina. The free surface is rough and villous.

Trichosurus vulpecula.

The stomach differs from that of *Phascolarctos* in the following respects:—

1. It is more globular.
2. There is no sacculus on the greater curvature, but the stomach projects to the right of the pylorus.
3. The gland-patch is not present on the lesser curvature.
4. The pylorus is not such a well-defined cylinder, and does not project into the duodenum as in Man and *Phascolarctos.*
5. The walls of the stomach are relatively thinner.
6. The mucous membrane is rough, but has no rugæ.

In a hitherto unpublished note Garrod states that the fundus of *Cuscus maculatus* has a reticulum of rugæ.

THE INTESTINES.

Phascolarctos cinereus.

The external and internal characters have been fully described by Forbes and Chalmers Mitchell (**9**), and I have nothing to add to their accounts. My measurements differ greatly, however, from those recorded by various authors. The figures in the following table represent inches, and the asterisks denote that fresh specimens were examined. Lönnberg's specimen was a mammary fœtus *. If due allowance is made for shrinking induced by preserving fluids, it will be seen that the lengths of the different parts of the intestinal tube vary greatly in individuals, and have no relation to the length of the animal:—

	Length of animal.	*Small intestines.*	*Large intestines.*	*Cæcum.*
*Knox (1826)......	23	92	128	77
Martin (1836) ♀.	not given	not given	76	50
Owen (1837)......	23	92	125	77
*Forbes (1881) ♀.	17	115	93·25	46·75
Forbes (1881) ♀.	20·5	111·5	160·8	66
Lönnberg (1902).	3·5	14·55	11·45	3·4
*Sonntag (1921)...	21	54·5	75	36

Lönnberg (**17**) compared the measurements of the different parts of the intestinal tract of *Phascolarctos* and several other Marsupials, and he also compared those of the fœtal and adult intestines, taking Forbes's figures as the standard for the latter. He came to the following conclusions:—". . . . the difference is quite striking with regard to the cæcum and the large intestine. The former is proportionately only about a third as long in the fœtus as in the full-grown animal, and the latter less than half as large in the fœtus as in the adult. The difference of the small intestine in both stages is not so great, that of the fœtus being about four-fifths of the same in the adult. It is also to be remarked that in the fœtus the small intestine is considerably longer than the colon, but in the adult the reverse is the case. The differences can of course be ascribed to the difference of the diet of both stages. The milk food of the mammary fœtus is chiefly or completely digested in the small intestine, but the vegetable diet of the adult needs a greatly developed cæcum and colon. The longitudinal folds of the cæcum and colon are, however, already developed in the fœtus."

---

* The mammary fœtus is the new-born animal fixed to the nipples in the pouch.

It is possible that the growth of the intestinal tract in my specimen has been considerably retarded.

Ellenberger, Tullberg, and Lönnberg believe that the large size of the cæcum in many animals, such as the Horse, Koala, and some Rodents, is brought about by the presence of a large amount of cellulose in the diet; and when the small intestine deals with all the elements of the food, there is no specialisation in the cæcum and colon. Lönnberg also speculates about the great length of the small intestine in phyllophagous Mammals. He states that the leaves consist of cellulose and certain protoplasmic, amylaceous, and other substances contained within resistant envelopes. Some time must elapse, therefore, before these are broken down and their contents become available for digestion and absorption; the small intestine is, consequently, long.

Lönnberg's views, however, will not account for the conditions present in the intestinal tract of the phyllophagous Three-toed Sloth (*Bradypus tridactylus*). In my paper dealing with its anatomy (**18**), I showed that the intestinal tract is short, the cæcal pouch is rudimentary, and the interior of the colon and rectum offers a large absorptive area, due to the excavation and folding of the mucous membrane; it possesses sphincters which are similar in character to, but larger than, those of the cæcum of *Trichosurus vulpecula*, and its muscular coat, which thickens from before backwards, may have a similar function to that of the cæcum of *T. vulpecula*.

Although the stomach of *B. tridactylus* contains many hard, almost entire leaves, the intestinal tract contains none, so the cellulose and hard materials have been completely comminuted and reduced to the state of chyme; Rapp's analogies are interesting in this connection, for he likens the paunch and pylorus to a crop and gizzard. This thorough digestive process must throw less work on the small intestines, which, in consequence, are short.

The chyme yields a number of substances for absorption in the small intestines, and the remainder is absorbed from the large intestines, whose pockets and sphincters retain it in the colon and rectum, and the muscular coat moves it backwards and forwards; and the sphincter ani has a retaining function similar to that of the septa higher up in the colon.

The differences between these two phyllophagous Mammals must therefore be due to complexity of the stomach and the different varieties of specialisation of the interior of the colon and rectum, but the increased internal surface of the colon and rectum of the Sloth is compensated for by the large size and great length of those of the Koala. The Langurs are intermediate in the complexity of their intestinal tract between the Sloth and Koala.

In *Phascolomys mitchelli* the cæcum is considerably reduced, and Lönnberg believes that the colon has become considerably enlarged to take on the cellulose-digesting function of the cæcum. The stomach is simple as in the Koala, so it has not had any modifying influence on the complexity of the intestinal tract as in the Sloth. The Wombat has external sacculi, but the Sloth has internal cavities, so there is a greater similarity between their colons than exists between the colon of either of these animals and that of the Koala.

I have already shown how the complexity of the stomach is also influenced by the degree of development of the buccal organs (**19**). One must take a wide view of the whole alimentary canal from mouth to anus in framing an explanation of the physiology of any one part.

THE URINARY ORGANS (text-fig. 61).

Phascolarctos cinereus.

The *right kidney* is 3·2 cm. long, 1·8 cm. wide, and 1·6 cm. thick; it lies entirely anterior to the *left kidney*, whose corresponding measurements are 3·7, 2·4, and 1·5 cm.; its hilum is ventral in position, whereas that of the left kidney is mesial. The structures in the hilus have the usual disposition in regard to one another.

On section each kidney is seen to possess a thin cortex, and a single large papilla.

The surface of each renal pelvis and hilus is covered by a plexus of small veins. These communicate posteriorly with the veins ascending along the ureter, and they open anteriorly into the renal vein.

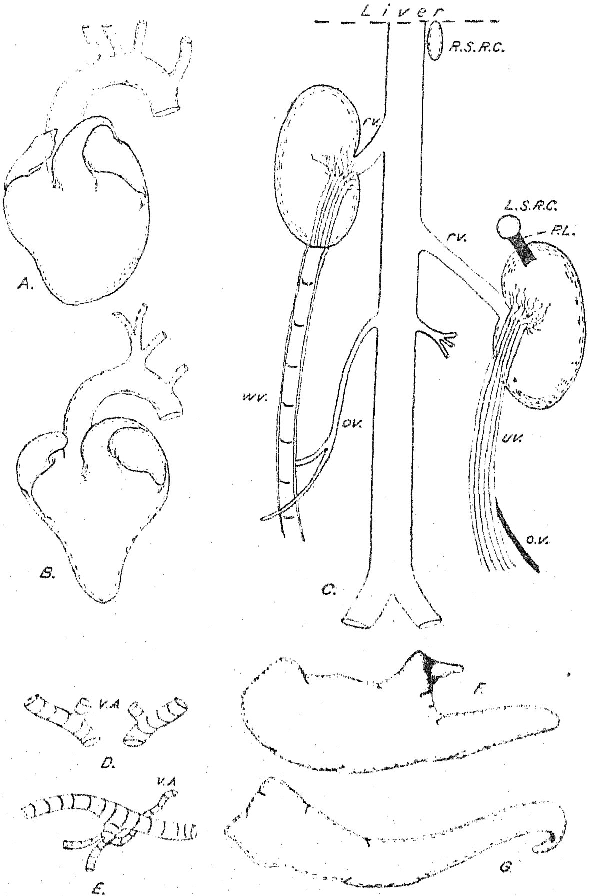
The *right ureter* lies parallel to, but 1 cm. to the right of, the vena cava inferior. It passes ventral to the iliac vessels and runs posteriorly along the dorsal pelvic wall. It opens into the lower and back part of the bladder.

It is accompanied by small veins from the pelvis; the latter are joined by veins from the ovaries, after which a ladder-like arrangement of veins runs up to the venous plexus on the ventral surface of the renal pelvis (text-fig. 61 C, *wv*).

The *left ureter* runs along the left border of the abdominal aorta, crosses the iliac vessels, and courses through the pelvis as does the right one. The veins accompanying it are numerous and some of them ramify; so dense is the venous plexus that the ureter is concealed by them. At first sight it looks like a cord of veins.

John Hunter (22) showed that the relative positions of the kidneys of *Petaurus taguanoides* are similar to the above.

Text-figure 61.



A. heart and aorta of *Phascolarctos cinereus* with origins of right subclavian, right common carotid, left common carotid, and left subclavian arteries, from right to left, and described in text as *a*, *b*, *c*, *d*: B. heart and aorta of *Trichosurus vulpecula*: C. kidneys and some of the abdominal veins: L.S.R.C. and R.S.R.C., suprarenal capsules; P.L., peritoneal ligament: D and E. origins of vertebral arteries in *Phascolarctos cinereus* and *Trichosurus vulpecula* respectively: F and G. spleens of *Trichosurus vulpecula* and *Phascolarctos cinereus* respectively.

The *bladder* is pyriform and firm, but no urachus is seen. Lateral peritoneal folds connect it to the pelvic wall, but no other ligaments are present.

Trichosurus vulpecula.

The anterior half of the right kidney is received into a deep recess in the liver, and its posterior pole is level with the hilus of the left kidney. The bladder is transversely corrugated on the surface and no urachus is present. Only one wide renal papilla is present in each kidney.

GENERATIVE ORGANS.

I have nothing to add to existing accounts of the generative organs of either species.

THE PANCREAS.

The duct is dead-white in *Phascolarctos* and shines through the translucent brown glandular tissue. The latter in my specimen has the same appearances as those described by Martin (**8**).

THE LIVER.

Phascolarctos cinereus.

Forbes (**4**) described and figured the liver, and Braus (**1**) described its histology.

The *hepatic artery* is very convoluted, and divides into two terminal convoluted branches which diverge at the sides of the gall-bladder. From the left branch a straight, slender cystic artery runs in the free edge of the vesical mesentery to the gall-bladder, which it reaches about its middle; then it runs posteriorly along the surface of the gall-bladder as far as the fundus.

The *postcaval vein* is never deeply embedded in the hepatic substance, and receives three hepatic veins at its emergence from the anterior surface of the liver. A fourth vein enters it within the organ.

The *common bile-duct* does not exhibit cysts of its mucous membrane similar to those of some Marsupials described by Owen (**11**).

Trichosurus vulpecula.

The liver differs from that of *Phascolarctos* as follows:—1. It is not so compressed antero-posteriorly. 2. Its edges are not notched by many small fissures. 3. The hepatic tissue is not so subdivided. 4. The right lobe recesses the anterior half of the right kidney. 5. The gall-bladder is shorter and broader, and only projects for a short distance into the abdominal cavity beyond the posterior edge of the right lobe when fully distended with bile.

THE DUCTLESS GLANDS.

Phascolarctos cinereus.

The *Thyroid Gland* (text-fig. 56, A, A).—The two lateral lobes are unconnected, and vary in shape and extent. The *left lobe* is pyriform, with the broad extremity posterior and slightly within the thorax. It is 2 cm. long, ·8 cm. wide, and ·3 cm. thick. It is separated from the larynx by the first three tracheal rings. The *right lobe* is elongated and ovoid, and measures 2·7 × ·5 × ·3 cm. Its anterior extremity overlaps the lower end of the larynx, and its posterior pole stops anterior to the thorax. The *arterial supply* comes from the thyroid and laryngeal branches of the common carotid artery (*m*), and the *veins* run to the internal jugular vein (*n*).

I did not observe any structures which could be definitely described as *parathyroid bodies*, but they may have been lying among the small glands which are numerous at the root of the neck.

The *Thymus Gland* has been described by Symington (**15**).

The *Suprarenal Capsules* (text-fig. 61, S.R.C.).—The left capsule is a round body, of the size of a large pea, lying on the mesial aspect of the anterior pole of the left kidney, to which it is attached by a fold of peritoneum. The right capsule is oval, and has a peculiar position; it lies in contact with the posterior surface of the liver, and is situated between the inferior vena cava to the right, the right crus of the diaphragm to the left, and the œsophagus ventrally.

The greater part of each capsule is composed of brown medulla.

The *spleen* has been described by Martin (**8**).

My specimen is triangular and measures 7·4 cm. long, but that of *Trichosurus vulpecula* has a lateral process (text-fig. 61, F and G). In *Phascolomys* it is an equilateral triangle.

Trichosurus vulpecula.

The lateral thyroid lobes (text-fig. 57 A) measure 1·3 cm. long and ·3 cm. wide. They lie at the sides of the posterior extremity of the larynx and anterior seven tracheal rings. The connecting isthmus crosses rings 5, 6, and 7.

The thyroid artery describes a curve, with the convexity forwards, and runs along the anterior five-sixths of the mesial border of its corresponding lateral lobe. The thyroid vein runs to the internal jugular vein (*p*). This arrangement of the thyroid vessels is seen in animals belonging to several of the Mammalian orders.

THE ORGANS OF CIRCULATION.

Phascolarctos cinereus.

The Heart (text-fig. 61, A).—The fibrous pericardium is firmly bound to the dorsal surface of the sternum and left ribs by connective tissue. It narrows out and is lost on the great vessels. These conditions are also present in *Trichosurus vulpecula*. The area of adhesion is greater than that of *Dendrolagus ursinus*.

The long axis of the heart is antero-posterior and parallel to the left side of the sternum, and the apex is level with the posterior border of the fourth left costal cartilage. Its apex is more obtuse than that of *Trichosurus vulpecula* *.

Measurements :—

	Phascolarctos.	*Trichosurus.*
Length	4·6 cm.	3 cm.
Greatest width	2·4 ,,	2·2 ,,
Greatest thickness ...	1·9 ,,	1·5 ,,

The characters agree with those already described for the Marsupial heart.

The *Ascending Aorta* (text-fig. 61 A) is embraced by the two parts of the right auricular appendix, and is parallel to the right precaval vein. It quickly gives way to the *aortic arch*, whose most anterior point is level with the anterior end of the first intercostal space. At the level of the fourth dorsal vertebra it gives way to the descending aorta; this is the commonest level for the transition in the Mammalia. The relations of the arch are :—

Ventral.—Left lung, left precaval vein, left azygos vein, left vagus nerve, left phrenic nerve.

Dorsal.—Trachea, œsophagus.

Posterior.—Root of left lung.

Anterior.—Great vessels of head, neck, and fore limbs. Branches :—The right subclavian (*a*), right common carotid (*b*), and left common carotid (*c*) arise directly, and close to one another, from the aortic arch, so there is no innominate artery. After a short interval the left subclavian artery is given off (*d*). Martin (**8**) and Owen (**11**) describe an arrangement similar to that of Man, but Forbes (**4**) states that the innominate artery gives off three vessels close together from a common trunk. In *Trichosurus vulpecula* the aortic arch gives off the innominate and left subclavian arteries, and the former, after giving off the left common carotid, divides into right common carotid and right subclavian arteries; the left common carotid arises almost at the beginning of the innominate artery.

The *Common Carotid Arteries* give off fine entocarotids at the level of the anterior border of the hyoid bone, and are continued as stout ectocarotids. The former give off no branches in the neck, and enter the carotid foramen in the basisphenoid. The latter pass antero-laterally between the exoccipital process and the mandible, and the former separates it from the external jugular vein. In *Trichosurus vulpecula* the exoccipital process does not separate these vessels.

---

* Some specimens of *Trichosurus vulpecula* have a more obtuse cardiac apex than the above.

The *Descending Thoracic Aorta* lies first on the right half of the body of the fifth dorsal vertebra, but passes more to the right as it runs backwards through the thorax. It is connected to the œsophagus by a triangular fold of pleura, whose base is attached to the diaphragmatic pleura. It has the usual relations and gives off the usual branches.

The *vertebral arteries* come off from the subclavians, but in my specimen of *Trichosurus* they arise from axes (text-fig. 61, E).

The Abdominal Aorta differs from the common Marsupial condition in that it is entirely to the left of the postcaval vein. Hochstetter (**20**) examined several species, and found that the postcaval vein concealed the lower end of the aorta in all but *Petaurus taguanoides*, but he did not include *Phascolarctos cinereus* in his list. Beddard (**21**) also found the postcaval vein covering the aorta in all his species. My observations on *Trichosurus vulpecula* and *Dendrolagus ursinus* confirm those of Hochstetter and Beddard.

Relations.—At the point where the abdominal aorta reaches the level of the posterior surface of the liver, it is separated from the right suprarenal capsule by the right crus of the diaphragm. These structures separate it from the postcaval vein.

A little posterior to the capsule the solar plexus lies between the aorta on the left, the postcaval vein on the right, and the cœliaco-mesenteric artery ventrally.

Posterior to the solar plexus the postcaval vein lies immediately to the right side of the aorta till the latter divides into the internal iliac and mid-sacral arteries, and then the vein crosses the surface of the aorta. The whole trunk of the aorta is visible.

The relations to other structures show nothing unusual.

Branches.—With the exception of the four pairs of *lumbar arteries* which arise at regular intervals from the sides, the following is the order of the branches from before backwards:—

Phrenics, cœliaco-mesenteric, suprarenals, renals, ovarians, external iliacs, internal iliacs, and middle sacral (caudal).

After giving off the external iliac arteries, the trunk of the aorta diminishes in calibre to a little more than half of that of either of the external iliac arteries.

The *Cœliaco-mesenteric Artery* divides into cœliac axis and anterior mesenteric artery, and a branch of the latter replaces the posterior mesenteric branch of the abdominal aorta of the higher Mammalia.

The *cœliac axis* divides into gastric, hepatic, and splenic arteries, whose distribution has already been described.

The *anterior mesenteric artery* describes a curve, convex forwards and to the right, and terminates in the cæcum; it occupies the free edge of the cæcal mesentery in the latter part of its course.

The branches supplying the large intestines arise from the convexity of the curve, and those destined for the small intestines are given off from the concavity. The highest branch anastomoses with the duodenal branches of the hepatic artery, and the lowest one anastomoses in the pelvis with the hæmorrhoidal vessels. The lowest branch to the ileum anastomoses with the branches to the cæcum.

The mesenteric areas between the branches of the mesenteric artery contain rich networks of fine lymphatic vessels, and fine branches of the solar plexus accompany the arteries. The *mesenteric veins* have been figured already by Chalmers Mitchell (**9**).

In *Trichosurus vulpecula* the cœliac axis arises separately.

THE VEINS.

The *Anterior and Posterior Facial Veins* have the usual formation, course, and tributaries. They unite to form the *external jugular vein* on the surface of the exoccipital process. The latter runs postero-mesially across the sternomastoid to reach its lateral border in the posterior sixth of the neck. It passes dorsal to the posterior end of the sterno-mastoid and clavicle, and, anterior to the neck of the first rib, it unites with the axillary vein to form the precaval vein. Both veins are united by a long **V**-shaped vena transversa. In *Trichosurus vulpecula* the vein is more transverse (text-fig. 55).

Tributaries.—Auriculo-temporal, acromial, transverse scapular, muscular, ascending cervical and internal jugular veins. These vessels have the usual distribution. No anterior jugular vein is present.

The *vena transversa* receives veins from the tongue, submaxillary glands, and muscles of the mylo-hyoid region.

At the point where the internal and external jugular veins unite there are several small glands.

The *innominate and precaval veins* follow the usual course of the Marsupial type, and the *azygos veins* in my specimen are similar to those described by Forbes (**4**). The intrathoracic part of the *postcaval vein* measures 1·5 cm.

The *postcaval vein* is formed in the usual manner, but the only part lying ventrally superficial to the abdominal aorta crosses the termination of the latter. This arrangement is an exception to Beddard's statement that "the Marsupials show a very constant condition in that the postcava lies medianly ventral to the aorta, so that on dissection the aorta is not seen, being completely covered by the postcava" (**21**).

It lies to the right side of the aorta, and close to it till it reaches the right renal vein. After that it bends to the right and enters the liver. At the point where it disappears from view it is in contact with the right suprarenal capsule, and is accompanied by twigs from the right half of the solar plexus.

The *left ovarian vein* (text-fig. 61 C, *ov.*) joins the thick venous plexus running along the ureter; therein it is united to veins ascending from the pelvis. The *right ovarian vein* communicates with the right ureteric veins by a stout trunk, and then runs forwards to join the postcaval vein. The *ureteric veins* (*uv.* and *wv.*) form a plexus on the ventral surfaces of the renal pelves and open into the renal veins (*rv.*).

The Nervous System.

The *brain* has been described by Owen (**11**), Forbes (**4**), Elliot Smith (**12**), and Ziehen (**14**), and I have nothing to add to their accounts.

The Vagus Nerves (text-figs. 62 and 63).

Phascolarctos cinereus.

A short distance posterior to the base of the skull the vagus nerve on each side receives the hypoglossal (XII.) nerve, and their fibres intermingle in a very thorough manner. Soon they separate again, and the vagus runs postero-mesially as far as the anterior extremity of the thyroid cartilage, where it unites with the cervical sympathetic cord (C.S.) to form a vago-sympathetic (V-S.). A short distance anterior to the clavicle it separates again into vagus (V.) and sympathetic (S.).

This arrangement is present in most of the Carnivora. It differs from that of *Dendrolagus*, in which the vagi and sympathetics remain separate.

There is no trace of the ganglion of the trunk of the left vagus (ganglion nodosum) in the neck. The right nerve has one (G.N.).

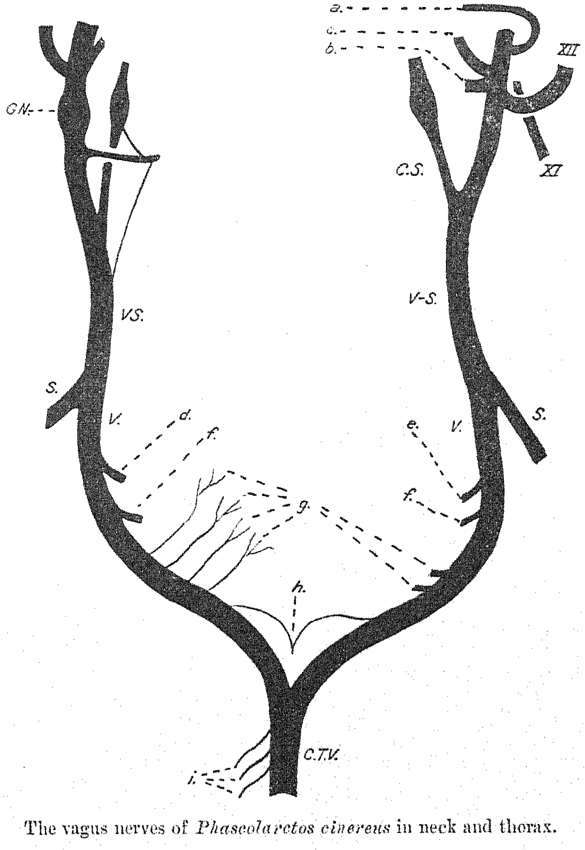
Branches in the neck.—Pharyngeal (*a*), anterior laryngeal (*b*), communicating to the first cervical nerve (*c*), and recurrent branch of the right vagus (*d*).

The relations of the vagi in the thorax differ. The *left nerve* crosses superficial to the left subclavian artery and aortic arch, lying on the inner side of the left precaval vein and left phrenic nerve, and on the outer side of the trachea, œsophagus, and left common carotid artery. It passes dorsal to the root of the left lung and gains the dorsal aspect of the œsophagus. The *right nerve* crosses the right subclavian artery under cover of the right precaval vein, runs down the side of the right main bronchus, and gains the dorsal aspect of the root of the right lung; lastly it passes to the dorsal aspect of the œsophagus, where it fuses with the left nerve to form the combined trunk of the vagi (C.T.V.).

Branches of the separate nerves in the thorax.—Left recurrent laryngeal nerve (*e*), cardiac (*f*), pulmonary (*g*), and a branch from each nerve which unites with its neighbour to form a fine cord, which runs posteriorly along the ventral surface of the œsophagus (*h*).

The combined trunk of the vagi enters the abdomen dorsal to the œsophagus, runs dorsal to the stomach, and ends in the left half of the solar plexus. It gives off ventral gastric nerves in the thorax (*i*), and stout ventral (*j*), and strong dorsal (*k*), gastric nerves in the abdomen.

Text-figure 62.

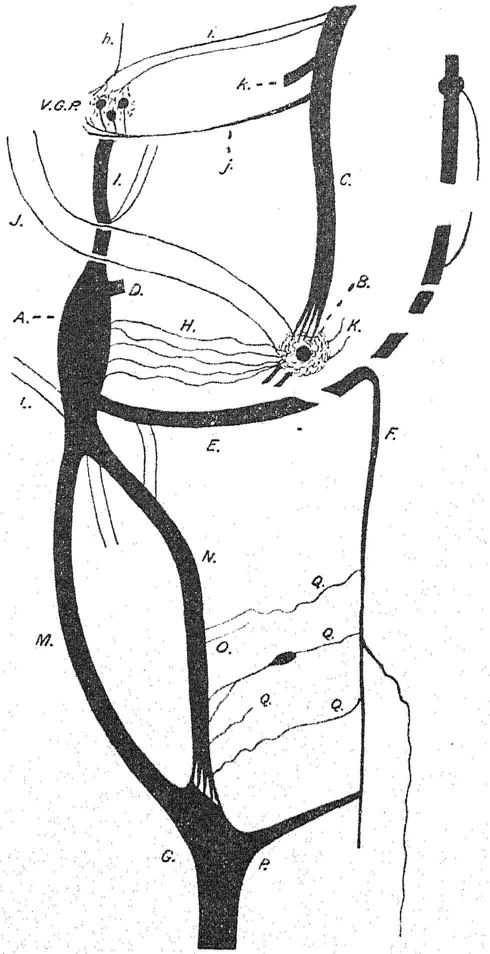


The vagus nerves of *Phascolarctos cinereus* in neck and thorax.

It is possible that sympathetic filaments run anteriorly from the solar plexus to the stomach in the combined trunk of the vagus, for it has been shown that sympathetic filaments run in other nerves (*e. g.* the sciatic).

The two halves of the solar plexus (text-fig. 63) lie between the abdominal aorta and postcaval vein under cover of the origin of the cœliaco-mesenteric artery. The right half (A) is a fusiform ganglion, but the left half (B) consists of a nerve plexus with a small round ganglion. The combined trunk of the vagi (C) enters the left half of the plexus by a brushwork of nerves. The right and left sympathetic nerves (D and E) end in the right half of the plexus, but the left sympathetic gives off

Text-figure 63.



The vagus nerves and abdominal sympathetic of *Phascolarctos cinereus.*

a fine nerve (F), which enters into the formation of the aortic plexus farther back (G). Fine fibres (H) connect the halves of the plexus.

Branches of distribution :—

1. Three nerves which course along the postcaval vein and embrace the right suprarenal capsule (I).
2. Hepatic plexus (J).
3. Splenic plexus (K).
4. Right renal plexus (L).
5. Two cords (M and N) which emerge from the posterior end of the right half of the plexus and form a loop lying dorsal to the postcaval vein. The left one breaks up into a number of fibres which reunite later with the right one, and it gives off the left renal plexus (O).

The loop unites with the left sympathetic by a T-shaped junction (P), and fine filaments (Q, Q, Q, Q) also run between them.

Only one cervical sympathetic ganglion—namely the superior one—exists.

SUMMARY.

The differences between *Phascolarctos* and *Trichosurus* may be summarised as follows:—

Phascolarctos.	*Trichosurus.*
1. Platysma myoides strong.	1. Platysma weaker.
2. No true hyoglossus muscle.	2. Hyoglossus present.
3. Vena transversa Λ-shaped.	3. Horizontal.
4. Absent.	4. Anterior jugular vein present.
5. Lateral organs of tongue look like glands.	5. Composed of fissures and laminæ.
6. One vallate papilla.	6. A vallate triangle.
7. Plicæ fimbriatæ present.	7. Sublingua well developed.
8. Cheek-pouches present.	8. Absent.
9. All anterior palatal ridges transverse.	9. Anterior palatal ridges convex forwards.
10. Tongue far from epiglottis.	10. Close to epiglottis.
11. Epiglottis broad and entire.	11. Narrow and notched.
12. Gland-patch in stomach.	12. Absent.
13. Pylorus projects into the duodenum.	13. Pylorus does not project.
14. Tonsils far back in the pharynx.	14. Tonsils in fauces.
15. Pharynx has two dorsal ridges.	15. Absent.
16. Absent.	16. Dorsal ridge in nasal tube.
17. Cardiac apex obtuse.	17. More acute.
18. Absent in my specimen.	18. Innominate artery present.
19. Postcava crosses end of abdominal aorta.	19. Postcava conceals posterior half of aorta.
20. Liver more subdivided.	
21. Gall-bladder long and narrow.	21. Short and wide.
22. Right kidney posterior to liver, and each kidney has one conical papilla.	22. Sunk in liver, and each kidney has one broad, flat papilla.
23. Thyroid gland in posterior part of neck.	23. In anterior part.

Phascolarctos.	*Trichosurus.*
24. No thyroid isthmus.	24. Isthmus present.
25. Patella absent.	25. Patella thin and scale-like.
26. Absent.	26. Right lung has an azygos lobe.
27. Two lobes in each lung.	27. Left lung has two, and right has four lobes.
28. Spleen triangular, and has no lateral process.	28. Spleen has a lateral piece.
29. Vertebral arteries arise from subclavian arteries.	29. Vertebral arteries arise from an axis on each side.
30. Intestinal measurements much greater.	

Owen stated that the Koala is the Marsupial which has the greatest claim to typical pre-eminence. MacAlister, on the other hand, showed that it has more individual peculiarities in its myology than has any other Didelphian; and the remarks made in this paper show how many of the appearances of its internal organs are peculiar to itself, for several of those described for *Trichosurus vulpecula* are similar to the conditions present in many Marsupialia. There are also many striking differences between the external and skeletal characters of *Phascolarctos* and those of *Trichosurus*, but I have nothing new to add to existing descriptions.

Bibliography.

1. Braus, H.—Jen. Denkschr. Bd. 5 (Semon, Zool. Forschungsreisen, Bd. 2). Jena. G. Fischer, 1896.
2. Edelmann, T.—Deut. Zeitschr. f. Thiermed. Bd. xv. pp. 165–214. 1899.
3. Flower, W. H.—"The Comparative Anatomy of the Organs of Digestion of the Mammalia." Medical Times and Gazette, 1872, p. 645.
4. Forbes, W. A.—"On some Points in the Anatomy of the Koala." Proc. Zool. Soc. London, 1881, pp. 180–195.
5. Home, E.—"An Account of some Peculiarities in the Anatomical Structure of the Wombat." Phil. Trans. Roy. Soc. 1808, pp. 304–312.
6. Knox, R.—"On the Wombat of Flinders." Edinburgh New Philosophical Journal, vol. i. p. 104. 1826.
7. MacAlister, A.—"The Muscular Anatomy of the Koala." Annals and Magazine of Natural History, 1872, pp. 127–134.
8. Martin, W.—"Notes on the Anatomy of the Koala." Proc. Zool. Soc. London, 1836, pp. 109–113.
9. Mitchell, P. Chalmers.—"Further Observations on the Intestinal Tract of Mammals." P. Z. S. 1916, pp. 195–197.
10. Oppel, A.—Text-book of Comparative Microscopic Anatomy, vol. i. p. 291, and vol. iii. p. 308.
11. Owen, R.—Art. "Marsupialia" in Todd's 'Cyclopædia of Anatomy and Physiology,' vol. iii.

12. SMITH, G. ELLIOT.—Journal of Anatomy and Physiology, xxxiii. 1898, p. 30.
13. YOUNG, A. H.—Journal of Anatomy and Physiology, xiii. 1880, pp. 305–317.
14. ZIEHEN, T.—Jenaische Denkschr., Bd. vi. 1897, p. 98.
15. SYMINGTON, J.—Journal of Anatomy and Physiology, xxxiv. p. 226.
16. POULTON, E. P.—"On the Tongues of the Marsupialia." Proc. Zool. Soc. London, 1883, pp. 599–628.
17. LÖNNBERG, E.—"On Digestive Adaptations in the Marsupialia." P.Z.S. 1902, i. p. 12.
18. SONNTAG, C. F.—"A Contribution to the Anatomy of the Three-toed Sloth." P.Z.S. 1921, pp. 157–177.
19. SONNTAG, C. F.—"The Tongues of the Cercopithecidæ." P.Z.S. 1921, pp. 280–281.
20. HOCHSTETTER, F.—Morphol. Jahrb. xx. 1893, p. 626.
21. BEDDARD, F. E.—"On the Postcaval Vein and its Branches in certain Mammals." P.Z.S. 1909, pp. 496–526.
22. HUNTER, JOHN.—'Essays and Observations.' Edited by Richard Owen. 1861, p. 257.

EXPLANATION OF THE PLATES.

PLATE V.

A. The Palate of *Phascolarctos cinereus* with the cheek-pouches packed with wool and pins in the Eustachian Tubes.
B. The Palate of *Trichosurus vulpecula*.
C. The Palate of *Pseudochirus peregrinus*.

PLATE VI.

The Stomach of *Phascolarctos cinereus*.

A. The interior of the stomach.
B. The projection of the pylorus into the duodenum.

31. New Indian Drilid Beetles. By S. MAULIK, F.Z.S., Professor of Zoology in the University of Calcutta.

[Received May 11, 1921: Read June 7, 1921.]

(Text-figures 1–5.)

In the present paper four beetles from India of the Family Drilidæ are described. They are all characterized by the possession of extraordinarily developed lamellate terminal joints of both the maxillary and labial palpi. These joints, of both pairs of palpi, are similar in structure, and are of almost equal size. They naturally fall into two genera, and can be distinguished thus:—

Head almost as long as the pronotum, so that the eyes are distant from the front edge of the pronotum. Antennæ distant	*Lamellipalpus*, gen. n.
Head short, the eyes almost touching the front edge of the pronotum. Antennæ more or less approximate	*Lamellipalpodes*, gen. n.

LAMELLIPALPUS, gen. n.

The type of this genus is *Eugeusis nigripennis* Pascoe, from Burma. At the end of his description of this insect (Ann. Mag. Nat. Hist. xx. 1887, p. 10, t. i. f. 7) the author remarks: "The description is from a female; the male has probably flabellate antennæ, as in *E. palpator* Westwood" (the type of the genus *Eugeusis*). I have examined Pascoe's type; it is not a female, therefore his conclusion that the male has flabellate antennæ is not correct. Under this assumption he included his *nigripennis* in Westwood's genus *Eugeusis*, of which I have seen a specimen in the collection of the British Museum, and with which it is not congeneric. It is necessary, therefore, to erect a new genus for the reception of this species as well as two others in the collection of the British Museum.

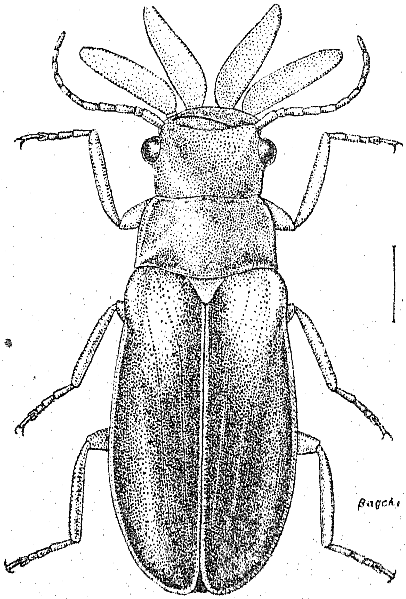
Generic characters.—The antennæ are 11-jointed, filiform; sometimes each joint is slightly expanded on the inner side. They are separated from each other by the whole breadth of the head, and are situated in front of the eyes. The eyes are convex and prominent. The mandibles are large, curved, and pointed; in repose they lie crossed. The maxillary and labial palpi are 4- and 3-jointed respectively, the terminal joint in each being very large, elongate, and compressed. The front coxæ are large and exserted, having a large trochanter; the intermediate and hind coxæ are contiguous, but not so large as the front ones. The tarsi are 5-jointed, the fourth being bilobed. The elytra are not of a membranous texture and the suture is closely fitting.

LAMELLIPALPUS NIGRIPENNIS Pascoe.

The following description and illustrations are from a fresh specimen taken by Mrs. Kemp in Assam :—

Colour testaceous brown; underside paler; elytra blackish, except an ill-defined basal area, the suture and the lateral margins; the antennæ except the two basal joints blackish; eyes deep black. The upper side of the head and prothorax is shining, the rest of the body being subnitid. The whole body of the insect is covered with fine brown pubescence.

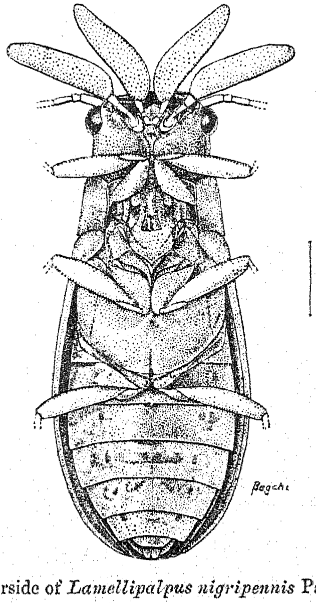
Text-figure 1.



Lamellipalpus nigripennis Pascoe.

Head almost as broad as long, slightly narrowed towards the neck, shallowly depressed in front; upper surface smooth, shining, sparsely covered with fine brown hairs. Viewed from above, the extraordinarily developed terminal joints of the palpi and the large mandibles are conspicuous. The joints of the antennæ are not at all expanded on the inner side. *Pronotum* broader than long, front margin straight, lateral and posterior margins slightly sinuate, anterior lateral angles rounded, posterior ones very acute. The upper surface is gently convex, shining, covered with fine brown pubescence, more so on the sides than on the middle area, deeply depressed at the base on either side of the longitudinal middle line. *Elytra* as broad at the base as the prothorax; the humeral angles are rounded. Corresponding to the basal depressions of the pronotum, the opposite elytral areas at the base are also depressed. The surface is punctate, covered with brown pubescence. Each elytron has four feeble costæ, the two inner ones—*i. e.*, those nearer the suture—being more prominent than the outer ones; the two inner ones commence at the base and terminate before reaching the apex; the third, commencing posterior to the humerus, terminates about the middle; the fourth, commencing below the humerus, terminates just beyond the middle. Of the four costæ the third is the feeblest; to a certain extent they converge towards the apex. *Scutellum* triangular, light brown, pubescent, impunctate, subnitid. *Underside* brown, but lighter than the colour of the upperside; the abdominal segments have a slight suffusion of black. The surface is sparsely covered with fine brown hairs, their roots give the surface an appearance of being finely punctate. The abdominal segments are at a lower level than the metathoracic segment; each is convex in the middle and depressed at the sides, these lateral depressions forming an oblique line on either side. The underside of the femora and tibiæ is not sulcate.

Text-figure 2.



Underside of *Lamellipalpus nigripennis* Pascoe.

Length 10 mm., breadth 4½ mm. Length of head 2 mm., breadth of head across the eyes 3 mm., without the eyes $2\frac{1}{2}$ mm. Length of pronotum $2\frac{1}{2}$ mm.

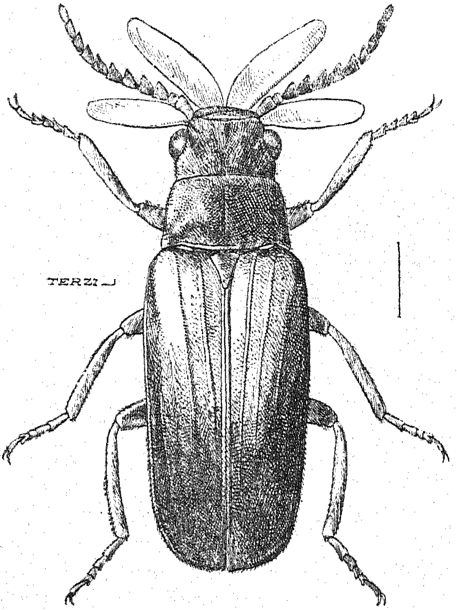
Assam, Garo Hills, Tura, 1400 ft.; Oct. 1917 (*Mrs. Kemp*) (Indian Museum).

The type specimen (Brit. Mus.) is from Burma. The brown parts in the type are lighter than Mrs. Kemp's specimen; also in the type the lighter colour of the suture and the lateral margins of the elytra is not so well marked.

LAMELLIPALPUS BOMBAYENSIS, sp. n.

Upperside shining, dark brown, in one specimen of the two lighter brown; the antennal joints from the third joint to apex brownish-black, and the apical area of the elytra obliquely continuing to the middle along the side smoky black; eyes deep black. Underside shining light to dark brown. The whole insect, both on the upper and lower sides, is covered with light brown pubescence.

Text-figure 3.



Lamellipalpus bombayensis Maulik.

Head almost as long as broad, depressed in the middle in front but convex round the roots of the antennæ; surface punctate, each puncture having a stiff hair. The eyes strongly convex.

The first joint of the antennæ club-shaped, the second very short, the third to the tenth almost equal in size and slightly expanded triangularly towards the inner side, the last joint bluntly rounded. In the expanded character of the several joints of the antennæ it bears a certain amount of resemblance to *Eugeusis palpator* Westwood, in which these points are extraordinarily expanded into rami. *Prothorax* about as broad as long, slightly narrowed towards the front; the posterior lateral angles produced to acute points; surface convex, with a faint longitudinal impression along the centre and deeply sloped on each side; this, with a similar slope on the elytra in front of the humerus, forms a deep depression; closely punctate. *Scutellum* triangular, punctate. *Elytra* as broad at the base as the prothorax. The lateral margins and suture costate. On each elytron there are three more or less prominent costæ; one runs close to the suture, the second along the longitudinal middle line, and the one nearer the margin starts from a point below the humerus, a feeble one, corresponding to the third in *Lamellipalpus nigripennis* Pascoe, is observable in certain lights. These costæ approach one another towards the apical area, where they disappear. The surface is irregularly punctate. *Underside* shining, smoother than the upperside.

Length 9–10 mm.

Bombay.

Described from two examples, the larger of which I have made the type specimen. It has the apical black patch on the elytra diffused, while in the other it is more sharply defined. In the type specimen the lamellate joints of the palpi are broader, with apex slightly narrowed, while in the smaller specimen they are uniformly narrower.

Type in the British Museum.

LAMELLIPALPUS MANIPURENSIS, sp. n.

Upperside subnitid, thorax and head more shining than the elytra; elytra and eyes black, the four lamellate terminal joints of the maxillary and labial palpi, and the antennal joints except a part of the two basal joints, smoky black; the rest of the body, including the underside, brown. The lamellate joints of the palpi are narrower and more elongate in this species than in the two others of this genus.

Head almost as broad as long; interantennal space shallowly depressed, covered with light brown pubescence. The first joint of the antennæ is almost as long as the third joint but very slightly thicker, second joint small and rounded, third joint slightly club-shaped, fourth to tenth almost equal to each other in length and thickness, the eleventh slightly longer than each of the preceding ones and rounded at the extremity; the joints of the antennæ are not at all expanded. *Prothorax* slightly broader than long, sides and front margin straight, basal margin sinuate; the posterior exterior angles acutely produced, the extreme edges of the produced part sharply depressed. The pronotum is covered with light brown erect pubescence. *Scutellum* brown, triangular, covered with light brown pubescence. *Elytra* almost as broad at the base as the prothorax. The surface is confusedly punctate and covered with light brown pubescence. The three costæ on each elytron are very feeble though distinctly recognizable. *Underside*: the elytra project to a certain extent beyond the abdomen, shining, covered with stiff brown hairs.

Length 7·5 mm.

Manipur (*Doherty*).

Described from one example.

Type in the British Museum.

LAMELLIPALPODES, gen. n.

The genus differs from *Lamellipalpus* in the length of the head and in the approximation of the antennæ, as has been indicated in the key given above. The type of the genus is the following species.

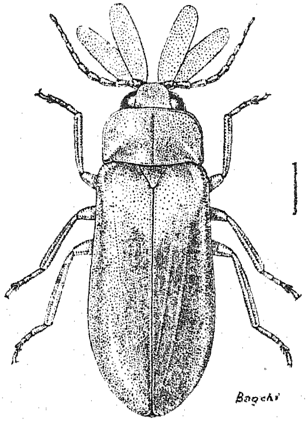
Although I include the two new genera described here in the family Drilidæ, I am not sure about the position of *Lamellipalpodes*, gen. n. When I examined *Lamellipalpus nigripennis* Pascoe (Garo Hills, *Mrs. Kemp*) and *Lamellipalpodes annandalei* Maulik at Calcutta, I was impressed by the fact that they both possessed the remarkable lamellate palpal joints but did not appear to belong to the same family. Dr. C. J. Gahan thinks that *Lamellipalpodes* Maulik does not belong to the Drilidæ, but is more allied to the Rhagophthalmidæ, a neighbouring family of about three genera, including nine species. Without further research it is not possible to decide this point.

LAMELLIPALPODES ANNANDALEI, sp. n.

Upperside yellow-brown, underside lighter; antennæ except the two basal joints, and the elytra except an ill-defined basal portion (which shares the colour of the pronotum) smoky black. Eyes deep black. The whole body is covered with brownish pubescence.

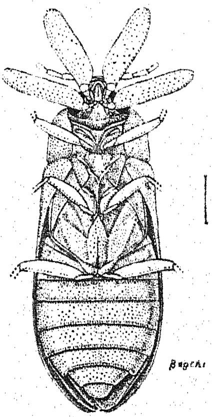
Head narrower than prothorax, the interocular space piceous. The first joint of antennæ stout and large, second joint very small and rounded, the third to the tenth similar in structure but of gradually diminishing length, the eleventh bluntly rounded. *Prothorax* broader than long, with a longitudinal median sulcation; posterior angles acute, pointed, anterior ones rounded; basal area depressed on either side of the middle longitudinal line, basal margin bisinuate. *Scutellum* triangular, with the apex rounded, brown, smooth. *Elytra* as broad at the base as the prothorax. Corresponding to the prothoracic depressions, the elytra are also depressed at the base. The surface neither smooth nor regularly punctate-striate. Each elytron is feebly tricostate; the costæ are more visible if the insect is held at certain angles; the first—that which is nearest to the suture—proceeds from the apex of the basal declivity of the elytra, the second commences from the edge of the elytral black area, the next commences about the middle of the elytron, each of these terminating on the apical area of the elytron.

Text-figure 4.



Lamellipalpodes annandelei Maulik.

Text-figure 5.



Underside of *Lamellipalpodes annandelei* Maulik.

Length 5¾ mm.

Described from five examples.

Type in the British Museum.

Cotype in the Indian Museum.

Of the five examples four belong to the British Museum, and these have only "Bengal" on the locality labels; the specimen belonging to the Indian Museum was taken by Dr. N. Annandale from the following locality:—

Barkuda Island, Chilka Lake, Ganjam district, Madras Presidency, 22. vii. 1920; found on bath-room window.

In this specimen the costæ of the elytra are more pronounced.

In preparing this paper I have had the advantage of seeing specimens in the British Museum collection. I wish to thank Dr. C. J. Gahan and Mr. K. G. Blair for their courtesy, valuable suggestions, and criticisms. I wish to thank also Dr. N. Annandale and Dr. and Mrs. Kemp for kindly letting me examine their respective insects. The drawings of two insects were made by Mr. S. C. Bagchi, of the Indian Museum, Calcutta, and of one by Mr. A. J. E. Terzi; to these artists my thanks are also due.

The preliminary study of these interesting beetles was made in the Indian Museum, Calcutta, while I held charge of its Entomological Section.

32. On some Abnormalities in the Carnivora. By Charles F. Sonntag, M.D., F.Z.S., Anatomist to the Society.

[Received May 10, 1921: Read May 10, 1921.]

(Text-figures 64–65.)

The following abnormalities were seen in animals dissected in the Society's Prosectorium during the past two years. They consist of:—

1. Elongation and contortion of vessels and nerves in the neck of a Bengal Fox (*Canis bengalensis*).
2. The occurrence of two separate precaval veins in a Panda (*Ailurus fulgens*).
3. Abnormal modes of termination of the vertebral veins of a Common Badger (*Meles meles*).

These conditions were compared with the normal state of the vessels, which is identical in all three animals.

The Normal Blood-vessels.

The aortic arch gives off the innominate and left subclavian arteries, and the former divides into the right subclavian and right common carotid arteries after giving off the left common carotid. The common carotid arteries run antero-laterally, and then straight forwards. The internal jugular veins are on their lateral aspects, and the vago-sympathetic nerve-cords lie on their dorsal surfaces.

The external jugular veins unite with the subclavian veins to form the innominate veins, of which the left one runs obliquely across the anterior part of the thorax and joins the more vertical right vein to form the precaval vein. The vertebral veins open by single trunks into the innominate veins.

The vena azygos major opens into the right side of the precaval vein immediately anterior to the root of the right lung.

Abnormalities in a Bengal Fox (text-fig. 64).

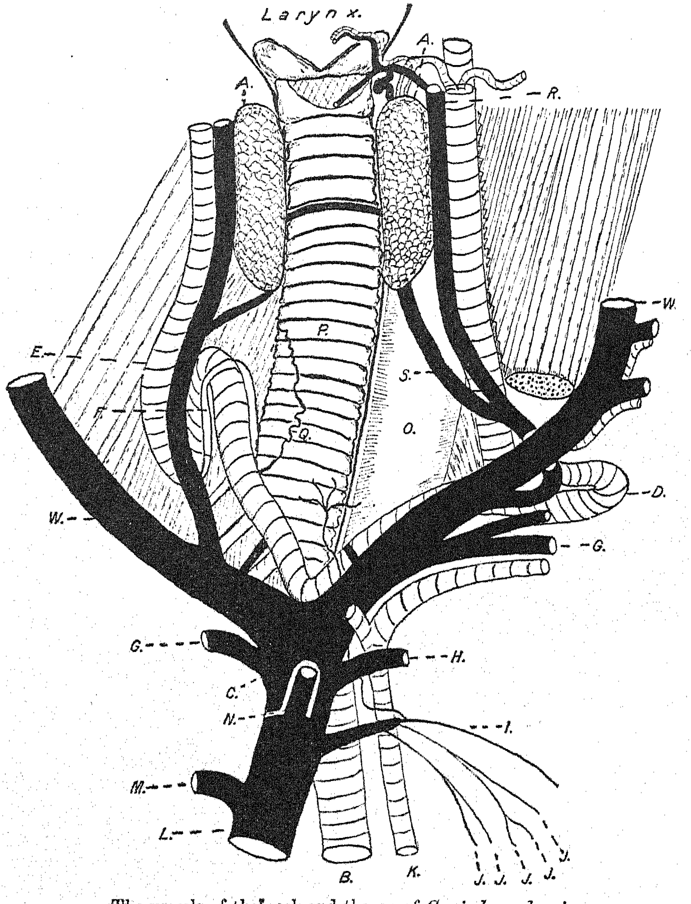
The animal, which was young, poorly-nourished, and rachitic, had a symmetrical and uniform enlargement of both lateral thyroid lobes (text-fig. 64, A.A), and the thymus gland was well-developed. The former were about twice the size of the lobes in a normal adult male. The isthmus of the thyroid gland was normal.

The innominate artery (B) divided in the normal manner, but the right subclavian artery was concealed by the right innominate vein (C).

The left common carotid artery (D) has a more horizontal course than the right one (E), and describes a very acute flexure with the convexity to the left. The right common carotid artery is not only flexed, but recurved, with the result that there is an **S**-shaped flexure. The left vago-sympathetic cord runs a straight course on the dorsal surface of the left artery, but the right cord (F) follows the right carotid in its wanderings, and appears on the surface for a short distance.

No growths or adhesions are present in the root of the neck which could be responsible for distortion of the vessels and nerves. All other vessels and nerves are normal as regards their course.

Text-figure 64.



The vessels of the neck and thorax of *Canis bengalensis*.
For explanation of letters see Text-figure 65.

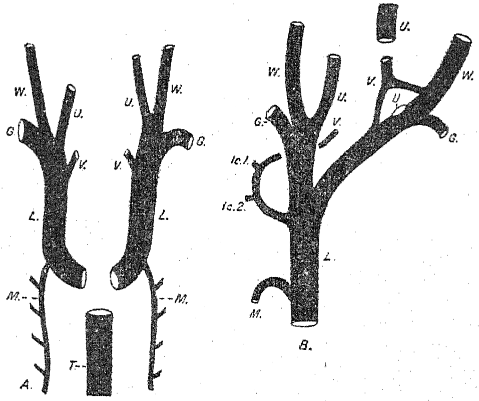
The precaval vein (L) receives internal mammary (N), pericardiac (J), and azygos veins (M), and a vein from the diaphragm running along the surface of the left phrenic nerve (I). No phrenic vein accompanied the right phrenic nerve.

The Occurrence of Two Precaval Veins in a Panda (text-fig. 65 A).

The innominate veins were formed as usual, but soon gave way to two precaval veins (L.L). The latter at first ran posteriorly and slightly mesially to points level with the anterior limit of the heart, when they turned directly inwards and ran horizontally; in this part of their course each vein receives an azygos vein (M). The orifices of the two precaval veins and the wide postcaval vein (T) form the angles of a triangle with the apex posterior.

This arrangement of the precaval and postcaval veins is the rule in Marsupials, but it occasionally occurs in higher Mammals. The chief difference between the condition described above and that of the Marsupials lies in the nature of the terminal orifices. In the latter the openings are closer together, and the postcaval and right precaval veins are only separated by a crescentic fold. In the former they are wider apart, and the crescentic fold is not present.

Text-figure 65.



The veins of *Ailurus fulgens* (A) and *Meles meles* (B).

Explanation of Letters.

G. subclavian veins; H. intercostal vein; Ic. 1 and Ic. 2. intercostal veins; O. œsophagus; P. trachea; Q. right recurrent laryngeal nerve; R. internal jugular vein; S. inferior thyroid vein; U. internal jugular vein; V. vertebral vein; W. external jugular vein. Other letters in text.

In the process of development the anterior cardinal veins from the head and the posterior cardinal veins from the body unite to form the Ducts of Cuvier, which open into the sinus venosus. The anterior cardinal veins become united by a transverse vessel, which takes a gradually increasing share in returning the blood from the left side of the head. Eventually the part of the left anterior cardinal vein between this vein and the sinus venosus atrophies, and the blood is conveyed entirely to the vein of the right side. The part of the right anterior cardinal vein between the cross vein and the sinus venosus becomes the precaval vein of the normal animal.

I believe that the persistence of two precaval veins in this animal is due to the non-formation of the cross vein.

No abnormality was found in the postcaval vein.

The veins of the father of this animal were quite normal.

Abnormalities in the Vertebral Veins of a Badger (text-fig. 65 B).

The left vertebral vein bifurcates in the lateral triangle of the neck; one of the divisions opens into the left external jugular vein, and the other one opens into the left innominate vein.

The right vertebral vein runs posteriorly dorsal to the right subclavian vessels, collects the veins from the first and second right intercostal spaces, and opens into the precaval vein.

33. The External Characters of the Koala (*Phascolarctos*) and some related Marsupials. By R. I. Pocock, F.R.S., F.Z.S.

[Received May 10, 1921: Read June 7, 1921.]

(Text-figures 22–26.)

CONTENTS.

	Page
Introduction	591
The Rhinarium	594
The Facial Vibrissæ	596
The Mouth	596
The Ear	596
The Fore Foot	599
The Hind Foot	601
The Pouch	604
The Classification of existing Diprotodonts	606

Introduction.

The body of the female *Phascolarctos* described in the following paper was very kindly sent to me by Mr. A. F. Richardson when I explained to him the zoological importance of the animal and the infrequency with which fresh examples come into the hands of anatomists in this country.

The need for renewed examination of *Phascolarctos* is especially shown by the disagreement amongst modern zoologists regarding the position and status to be assigned to it in the classification of Diprotodont Marsupials. Thomas, for instance (Cat. Marsupialia and Monotremata in Brit. Mus. 1888), divided the suborder into three families: (1) Macropodidæ with the subfamilies Macropodinæ, Potoroinæ, Hypsiprymnodontinæ; (2) Phalangeridæ with the subfamilies Tarsepedinæ (*Tarsipes*), Phalangerinæ (*Phalanger*, *Trichosurus*, *Pseudochirus*, *Petauroides*, etc.), and Phascolarctinæ (*Phascolarctos*); and (3) Phascolomyidæ (*Phascolomys*).

In connection with the Macropodidæ and Phalangeridæ, Thomas pointed out that the characters of *Hypsiprymnodon* are intermediate between those of the two families, and render the division between them by no means so sharp and well-defined as it has been usually considered to be. Nevertheless, his arrangement suggests that *Phascolarctos* is an aberrant member of the Phalangeridæ more nearly related to *Phalanger* than the latter is to *Macropus*.

Thomas's classification has been adopted by English zoologists and by Trouessart in his Catalogue (1912).

Bensley (Amer. Nat. xxxv. pp. 117–138 and 245–269, 1901; and Tr. Linn. Soc. Lond. (2) ix. pt. iii. pp. 83–214, 1903) followed Thomas in admitting the family Phascolomyidæ and in regarding *Phascolarctos* as the representative of a subfamily of the Phalangeridæ; but he made the important modification of transferring

Pseudochirus and *Petauroides* from the Phalangerinæ to the Phascolarctinæ because of the crescentic (subselenodont) pattern of the molar teeth in the three genera. Bensley's classification was adopted, presumably with approval, by W. K. Gregory (Bull. Amer. Mus. Nat. Hist. xxvii. pp. 215–216, 1910), who was acquainted with but rejected the classification by Winge quoted below.

Thomas, of course, was quite familiar with the dental character to which Bensley and Gregory attached so much importance. On p. 167 of his Catalogue he pointed out that by the complicated subselenodont character of its molars, *Pseudochirus*, with its close ally *Petauroides*, stands somewhat apart from most of the other Phalangers, and approaches *Phascolarctos*, in which a similar but simpler modification is observable. But his reasons for attaching to it subordinate systematic value lay apparently in the circumstance that in young examples of *Phalanger* a tendency towards the same structure is visible, but the crests on the molars soon wear off, leaving little difference between them and the simple quadricuspid molars characteristic of typical genera of Phalangeridæ. The obvious, but not on that account necessarily true, inference to be drawn from this fact is that the tendency towards the subselenodont molar pattern exhibited by *Phalanger* is a primitive character of the family Phalangeridæ, which is temporarily retained in *Phalanger*, lost in *Trichosurus*, *Dactylopsila*, and others, and elaborated in *Pseudochirus* and *Phascolarctos*.

Winge (E Museo Lundii, viii. pt. 1, 1893) held very different views. He adopted two families: (1) Phalangistidæ [=Phalangeridæ] with the subfamilies Pseudochirini for *Pseudochirus* and *Petauroides*, and the Phalangistinæ [=Phalangerinæ] for the two groups Phalangistæ (*Phalanger*, *Trichosurus*, *Petaurus*, *Tarsipes*, etc.), and Macropodes (*Macropus*, *Hypsiprymnodon*, etc.); (2) Phascolarctidæ with the subfamilies Phascolarctini (*Phascolarctos*) and Phascolomyini (*Phascolomys*)*.

Winge took as the basis for his classification the degree of extension of the tympanic process of the alisphenoid, which in the Phascolarctidæ (*Phascolomys*, *Phascolarctos*) is small, does not envelope the tympanic cavity, and fails to reach the paroccipital process, whereas in the Phalangeridæ, comprising the rest of the genera of Diprotodont Marsupials, the bone in question is large, envelops the tympanic cavity, and reaches the paroccipital process. As accessory characters, the vestigial tail, the presence of a cardiac gland in the stomach, and the loss of one of the two normal pairs of teats further serve to distinguish the Phascolarctidæ from the Phalangeridæ †.

---

* To these Winge added Thylacoleontini (*Thylacoleo*) related to Phascolarctini and Diprotodontini (*Diprotodon*, *Nototherium*) related to Phascolomyini.

† Winge's valuable paper is unfortunately written in Danish. The statements about the extension of the alisphenoid is taken from Max Weber's work. I have not been able to verify it in the case of the two skulls of *Phascolarctos* available for examination.

Attention may also be drawn to Winge's severance of the crescent-toothed or subselenodont Phalangers (*Pseudochirus* and *Petauroides*) from the rest as representing a special subfamily Pseudochirini equivalent to the Phalangerinæ containing not only the rest of the genera Thomas assigned to that subfamily, but all of those constituting the family Macropodidæ of that author.

Max Weber (Die Säug. p. 348, 1904) followed Winge in admitting the two families Phalangeridæ and Phascolarctidæ as he defined them; but he did not admit the subfamily groups Phascolarctinæ and Phascolomyinæ for *Phascolarctos* and *Phascolomys* respectively, and in the case of the Phalangeridæ he made a compromise between Thomas's and Winge's systems by dividing the family into three subfamilies: Phalangerinæ, Hypsiprymnodontinæ, and Macropodinæ.

It will be noticed that neither Winge nor Max Weber attaches any particular importance to the structural peculiarities of *Tarsipes*.

The divergence of opinion between the authors quoted may be briefly and more clearly expressed by the following tabulation of their classifications:—

Thomas. Family MACROPODIDÆ.
Subfamily MACROPODINÆ (*Macropus*, *Dendrolagus*, etc.).
„ POTOROINÆ (*Potorous*, *Bettongia*, etc.).
„ HYPSIPRYMNODONTINÆ (*Hypsiprymnodon*).
Family PHALANGERIDÆ.
Subfamily TARSIPEDINÆ (*Tarsipes*).
„ PHALANGERINÆ (*Phalanger*, *Trichosurus*, *Pseudochirus*, *Petauroides*, etc.).
„ PHASCOLARCTINÆ (*Phascolarctos*).
Family PHASCOLOMYIDÆ (*Phascolomys*).

Bensley. Family MACROPODIDÆ (*Macropus*, *Hypsiprymnodon*, etc.).
„ PHALANGERIDÆ.
Subfamily TARSIPEDINÆ (*Tarsipes*).
„ PHALANGERINÆ (*Phalanger*, *Trichosurus*, etc.).
„ PHASCOLARCTINÆ (*Pseudochirus*, *Petauroides*, *Phascolarctos*).
Family PHASCOLOMYIDÆ (*Phascolomys*).

Winge. Family PHALANGERIDÆ *.
Subfamily PHALANGERINÆ.
a. Macropodes (*Macropus*, *Hypsiprymnodon*, etc.).
b. Phalangeri (*Tarsipes*, *Phalanger*, *Trichosurus*).
Subfamily PSEUDOCHIRINÆ (*Pseudochirus*, *Petauroides*).
Family PHASCOLARCTIDÆ.
Subfamily PHASCOLARCTINÆ (*Phascolarctos*).
„ PHASCOLOMYINÆ (*Phascolomys*).

---

* For the sake of clearness in comparison, I have here altered the name *Phalangista* and its derivatives used by Winge to *Phalanger* and its derivatives.

Weber. Family PHALANGERIDÆ.
Subfamily MACROPODINÆ (*Macropus*, *Dendrolagus*, *Potorous*, *Bettongia*, etc.).
" HYPSIPRYMNODONTINÆ (*Hypsiprymnodon*).
" PHALANGERINÆ (*Tarsipes*, *Phalanger*, *Trichosurus*, *Pseudochirus*, *Petauroides*).
Family PHASCOLARCTIDÆ (*Phascolarctos*, *Phascolomys*).

External Characters.

The Rhinarium.—In *Trichosurus* the rhinarium is large, naked, and convex above; the infranarial portions are complete laterally and narrow; there is a median groove extending between the nostrils on to the philtrum, which is divided into two narrow strips, with a little process, overlying the gum between the median incisors, at the apex of the angular excision above. The nostrils are of the typical form, consisting of a rounded orifice in front, moderately widely separated from its fellow of the opposite side, and of a lateral and posterior narrow slit.

In *Phalanger* the rhinarium is in a general way similar to that of *Trichosurus*, but the nostrils are more widely separated, the infranarial portion is deeper in front, and the philtrum is exceedingly wide, and, although gradually narrowed below, is quite wide where it terminates on the edge of the upper lip. There is, moreover, no angular excision such as is seen in *Trichosurus*, but the median groove broadens below, its floor terminating in a median process which projects at least as low as the lateral portions of the philtrum.

In *Pseudochirus* the rhinarium is more like that of *Trichosurus*, but the infranarial portions are wider in front, with the inferior edge more steeply inclined; the median groove is continued between the nostrils to the summit of the rhinarium; and the inferior portion of the philtrum is quite narrow, with a small median notch.

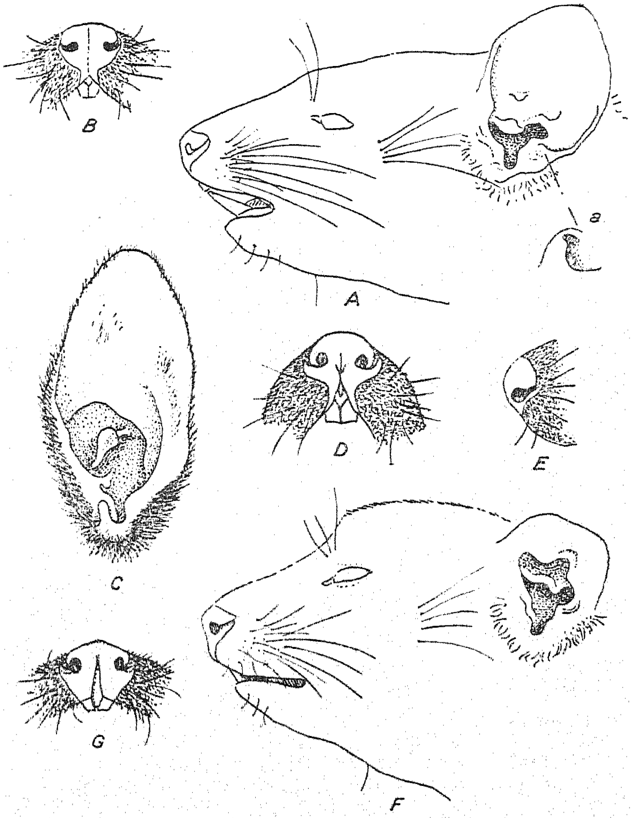
In *Phascolarctos* the nose is widely different. The muzzle is abruptly sloped downwards about an inch above the nostrils, and the whole of this inclined area is covered with very fine, short, scattered hairs, leaving a narrow, naked, thickened rim round the nostrils. Thus there is no true rhinarium. The nostrils themselves are also peculiar. Each consists of an ovally elongated valvular orifice, with a thickened superior and lateral rim, but with the inferior rim hardly defined from the upper lip; all trace of differentiation into lateral slit and anterior orifice has disappeared; the septum is very narrow, and is continued inferiorly between the two halves of the upper lip, ending below in a process over the gum between the median incisors.

In *Phascolomys ursinus* * the rhinarium is quite unlike that of *Phascolarctos*, and resembles, broadly speaking, the rhinarium of the three genera of Phalangers above described. It extends dorsally, however, further backwards in the middle line, and the hair of the muzzle encroaches over the well-developed slit of the nostrils, the expanded portions of which are widely separated in the middle line. The infranarial portions are moderately deep, and reach almost to the posterior end of the nostril-slits.

---

* The rhinarium of *Lasiorhinus latifrons*, the hairy-nosed Wombat, which should, I think, rank as a distinct genus, is unknown to me except from descriptions and a dried skin. It appears to differ solely from that of *Phascolomys* in being covered with short hair, the nostrils being normally formed.

Text-figure 22.



A. Head of *Pseudochirus peregrinus*, with pocket of ear (*a*) seen from above.
B. Rhinarium of the same.
C. Ear of *Trichosurus vulpecula*.
D. Rhinarium of the same, from the front.
E. Rhinarium of the same, from the side.
F. Head of *Phalanger maculatus*, the ear stripped of hair.
G. Rhinarium of the same, from the front.

Their inferior edge slopes obliquely downwards and inwards to the gum of the incisors, the two lobes of the upper lip being tolerably widely separable at this point. There is no median excision in the inferior edge of the rhinarium above the teeth, and there is no median groove, but a groove runs on each side from the nostril downwards and inwards to the gum, defining the infranarial portion from the rest of the rhinarium.

Facial Vibrissæ.—The facial vibrissæ are well and normally developed in *Trichosurus*, *Phalanger*, *Pseudochirus*, and *Phascolomys*, being represented by numerous long mystacials, superciliaries, genals—one tuft,—submentals, and interramals. In the examples of *Phalanger* and *Pseudochirus* examined, however, the interramals were few in number and slender. In *Phascolarctos* the vibrissæ are comparatively poorly developed, the mystacials especially being few and short and the interramal tuft wanting.

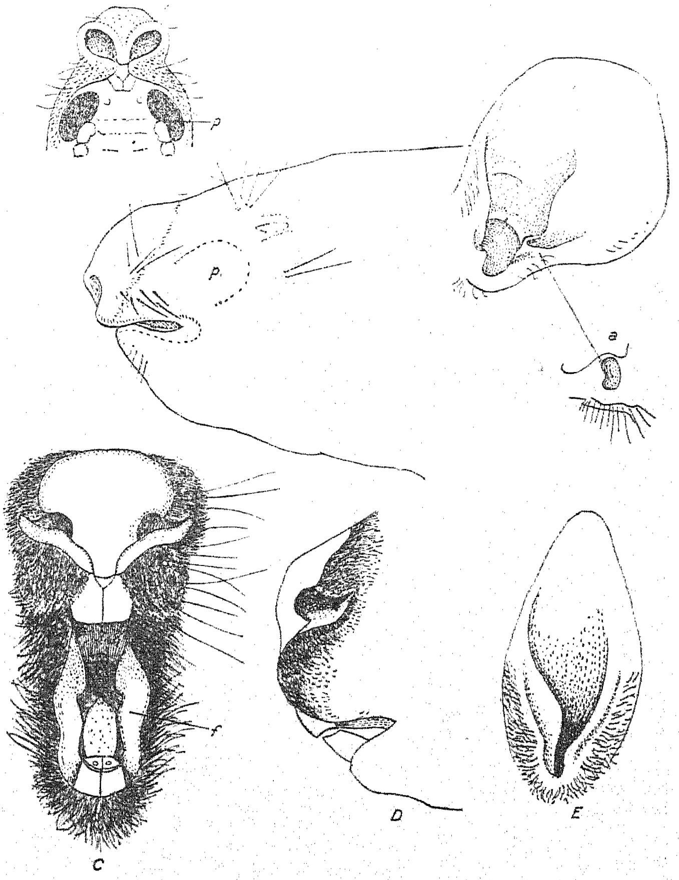
The Mouth.—There are only two points for me to notice in connection with the mouth. The first is the presence, with which everyone is familiar, of cheek-pouches in *Phascolarctos*. These lie alongside the gum of the upper jaw in front, the orifice looking downwards and the cavity extending upwards and backwards towards the eye. No such pouches occur in *Trichosurus*, *Phalanger*, *Pseudochirus*, or *Phascolomys*. The second is the presence in *Phascolomys* of a flap of naked skin extending into the mouth from the inner surface of the lips laterally. This is analogous to the similar ingrowths well known in the Rodentia, where they serve to close the throat during gnawing. Their function is no doubt the same in *Phascolomys*, which has rodent incisor teeth. These oral flaps of skin are not developed in the other genera here discussed, nor so far as I am aware in any other Marsupial.

a. A flap of skin jutting inwards from the lower lip and lying alongside the tongue on each side .... *Phascolomys.*
a′. No flap of skin jutting into mouth from the lips.
  b. A cheek-pouch on each side of the upper jaw .... *Phascolarctos.*
  b′. No cheek-pouches .... *Pseudochirus*, *Phalanger*, *Trichosurus.*

The Ear.—In *Trichosurus* the ear is high, but tolerably narrow and nearly naked internally. The supratragus (metatragus) is a well-developed thick, semicircular, slightly upturned disk. Above it there is a low curved ridge. In front of it the cavity of the ear is defined by a strong oblique ridge passing upwards slightly above the low ridge above described and inferiorly curving backwards beneath the supratragus and passing thence downwards on the inner side of the well-developed tragal thickening forming the anterior rim of the inferior notch (*aditus inferior*), the posterior border of which is defined by a strong thick antitragal ridge, capable of being turned outwards and backwards to a certain extent; but it exhibits no pocket-like depression.

In *Pseudochirus peregrinus* the ear is nearly as naked internally, and relatively nearly as high as in *Trichosurus* but somewhat broader. The supratragus is as well developed, but forms a more distinct roof to the deep lower portion of the cavity. The low ridge seen in *Trichosurus* is represented by a lobate thickening, and there is a similar thickening lower down behind, above the posterior end of the supratragus. The anterior ridge forms a lobate expansion above the anterior end of the supratragus, and the tragus itself is less well defined. The ridge behind the

Text-figure 23.



A. Head of *Phascolarctos cinereus*, with position of cheek-pouch (*p*) dotted in and pocket of ear (*a*) seen from above.
B. Nose and part of palate of the same, showing the nostrils and the orifices of the cheek-pouches (*p*).
C. Nose and mouth of *Phascolomys ursinus*, with lower incisors cut short and flap of skin (*f*) projecting into mouth.
D. Side view of rhinarium of the same.
E. Ear of *Lasiorhinus latifrons*, from dried skin softened in water.

inferior notch turns inwards above towards the posterior end of the supratragus, and it is provided with a shallow pouch defined externally by a definite thickened ridge.[*]

The ear of *Phalanger maculatus* is greatly reduced, thickly covered with hair externally, and scarcely projects above the level of the head. The supratragus is large and valvular, and the cavity of the ear above it is deep and roofed over by a ridge resulting possibly from the confluence of lobate thickenings homologous to the two seen in *Phalanger*. The anterior ridge does not extend so high above the supratragus as in the two genera already discussed, and there is a trace of the pouch on the posterior ridge, although it is not so well defined as in *Pseudochirus*.

In *Phascolarctos* the ear is more expanded even than in *Pseudochirus*, but it differs from the ear of that genus, *Trichosurus*, and *Phalanger* in having the supratragus reduced to a low curved ridge without any trace of the lobe[*]. There is a low ridge above it as in *Trichosurus*, and the anterior ridge bounding the cavity of the ear in front is as in that genus; the tragus, however, is much smaller. The pocket on the posterior ridge is present as in *Pseudochirus*, but is deeper and has a more sharply defined posterior rim.

In *Phascolomys* the antero-internal ridge, continuous above with the slightly overfolded anterior margin of the pinna, is produced inferiorly into a large compressed lamina, jutting backwards into the cavity of the ear and descending to the auditory orifice. Anteriorly and externally this lamina is marked by a deep groove which descends and passes into a low ridge defining the anterior border of the inferior notch, but there is no definite tragal thickening. The antitragal ridge is also simple. It ascends and forms the posterior edge of the cavity of the pinna, and is itself marked externally and posteriorly by a groove. The supratragus appears to be represented by a low ridge visible above the laminate expansion of the antero-internal ridge.

The ear of *Lasiorhinus latifrons* is very like that of *Phascolomys*, but is longer. On a skin softened in water I could find no trace of the supratragus.

The ear of *Phascolomys* resembles that of *Phascolarctos* in the complete or almost complete disappearance of the supratragus—an important character considering the constancy in the development of this ridge in many Mammals. But in the simple structure of the posterior antitragal ridge it is more like that of *Trichosurus*.

The differential characters of the ear may be used to define and classify the five genera as follows:—

a. Supratragus represented by a strong ridge with well-developed lobate thickening.
  b. No pocket above the antitragal ridge .... *Trichosurus*.

---

[*] Thomas mentioned this peculiarity and wrote "metatragus almost obsolete."

b'. A pocket above the antitragal ridge.
  c. Pinna greatly reduced; pocket small .... *Phalanger.*
  c'. Pinna large; pocket better developed .... *Pseudochirus.*
a'. Supratragus at most represented by a low curved ridge; without trace of lobate thickening.
  d. Antero-internal ridge normally developed; a large pocket above the antitragal ridge .... *Phascolarctos.*
  d'. Antero-internal ridge large and laminate; no pocket above antitragal ridge .... *Phascolomys.*

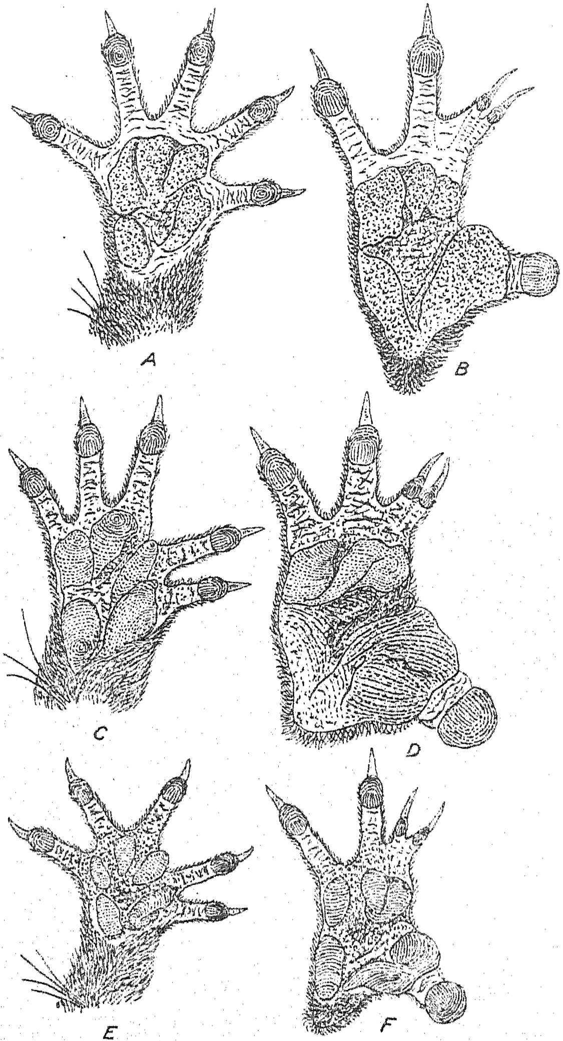
The Fore Foot.—In *Trichosurus*, *Phalanger*, and *Pseudochirus* there is a tuft of long carpal vibrissæ. In *Phascolarctos* and *Phascolomys* these tactile bristles are absent.

In *Trichosurus* the fore foot presents no special modifications. The five digits are free of webbing down to the plantar pads and are nearly evenly spaced, the third and fourth being the longest and subequal, the second and fifth a little shorter but subequal and rising at approximately the same level, and the first or pollex much the shortest, about two-thirds the length of the third or fourth, and not opposable but closing obliquely backwards and inwards across the sole (palm). The claws of all the digits are compressed, curved, and pointed, and the integument of the lower side of the digits is transversely grooved. The uniformly granular plantar pad is four-lobed, the three main lobes being in contact. The inner or pollical lobe, sometimes separated from the main lobes, is fused with the inner element of the carpal pad into a longitudinal mass, longer than wide. The external element of the carpal pad is elliptical, narrowly separated in front from the external lobe of the plantar pad, and, like the internal element, passes imperceptibly proximally into a narrow naked area of skin between them and the hair of the wrist. The centre of the sole is depressed and granular like the pads and the depressions between them.

In *Phalanger* the fore foot is considerably modified from the type seen in *Trichosurus*. The third, fourth, and fifth digits are evenly spaced; but the second is capable of being separated from the third by a much greater space than that between the third and fourth. With the pollex it is capable of being extended almost at right angles to the axis of the foot and of being closed transversely upon the sole. The pads are transversely striate, with the spaces between them granular, the space or groove between the second and third being deeper than that between the third and fourth. The first, the internal or pollical lobe, forms a continuous subtriangular mass, directed obliquely backwards and inwards when the pollex is drawn back, and the external moiety of the carpal pad is larger than in *Trichosurus*.

The capacity for co-operative movement of the first and second digits in a plane nearly at right angles to that of the third, fourth, and fifth seems to have been overlooked in *Phalanger maculatus*. Bensley, at all events, records the similar phenomenon in *Pseudochirus* and *Phascolarctos* as peculiar to these two genera. Nevertheless, the modification in question may be

Text-figure 24.



A, B. Right fore and hind foot of *Trichosurus vulpecula*.
C, D. „ „ *Phalanger maculatus*.
E, F. „ „ *Pseudochirus peregrinus*.
$\times \frac{1}{3}$.

clearly seen even on dried skins; and it is shown in the figures of the Spotted Cuscus in the Royal Natural History, iii. p. 257, 1894, and Harmsworth's Natural History, ii. p. 888, 1910. These figures bear the impress of having been drawn from life by Mützel and Kühnert respectively.

The fore foot of *Pseudochirus* resembles tolerably closely that of *Phalanger*, except that the third digit is not lengthened and the lobes of the plantar and carpal pads are separated and smaller, the fused pollical element of the plantar pad and the inner moiety of the carpal pad forming an oblique transverse mass about twice as wide as long.

The fore foot of *Phascolarctos* is an extreme exaggeration of the type seen in *Phalanger* and *Pseudochirus*, although the pads and intervening spaces are areolated or granular, not striated. The sole is much longer as compared with its width: the first and second digits are completely isolated from the rest, and rise close together from the postero-internal angle of the foot, at right angles to its long axis and close transversely across the proximal half of the sole, the posterior border of the pollex when drawn back being approximately in the same transverse line as the posterior border of the sole. There is a large three-lobed plantar pad at the base of the third, fourth, and fifth digits, and there is a similar but smaller lobe upon the base of each of the second and first digits. The one on the pollex probably represents the inner moiety of the carpal pad, and the one on the base of the second digit the first or external element of the plantar pad, widely severed from the lobe in front of it and altogether disconnected from the pollex behind it. The external moiety of the carpal pad is small, restricted to the postero-external angle of the foot and widely separated from the plantar pad.

In *Phascolomys* the fore foot, modified for terrestrial progression and digging, is very different from that of the preceding genera, especially from that of *Phascolarctos*. It may be derived from the type seen in *Trichosurus* by the shortening and widening of the digits and sole, the obliteration of nearly all trace of the individual elements of the pads, and by the straightening, lengthening, and blunting of the claws.

The Hind Foot.—In *Trichosurus**, *Phalanger*, and *Pseudochirus* there are one or two tactile vibrissæ, similar to the carpal vibrissæ, on the inner side of the heel behind the hallux. These are absent in *Phascolarctos* and *Phascolomys*.

The hind feet of the four arboreal genera—*Trichosurus*, *Phalanger*, *Pseudochirus*, and *Phascolarctos*—differ from each other much less than the fore feet. Their general structure is well known. Hence only the comparatively minor points of difference need be noticed.

---

* Represented in the figure of the hind foot of *Pseudochirus cooki* (pl. 20. fig. 4, of Waterhouse's 'Marsupiata'), but apparently unnoticed in the text.

In *Trichosurus* the conjoined second and third digits[*] are much shorter than the fourth. The three lobes of the plantar pad at the base of the terminal digits are in contact, the outer lobe being larger than the other two taken together. The large lobe of the hallux shows no trace of division, and there is a tolerably well-defined, long external metatarsal pad reaching from the heel almost to the plantar pad.

The digits of *Phalanger* are approximately as in *Trichosurus*; but the external lobe of the plantar pad is separated to a certain extent in front from the other lobes, which are fused although defined by a groove, and are together larger than the outer lobe. The entire hallux is relatively larger than in *Trichosurus*, and its great pad is indistinctly divided; there is no distinct external metatarsal pad and the heel is shorter than in *Trichosurus*.

In *Pseudochirus* the digits are as in the foregoing genera, but all the elements of the striated pads on the sole are better defined even than in *Trichosurus*. The outer lobe of the plantar pad is completely isolated from the two conjoined inner lobes and about half their size. The great pad of the hallux is distinctly divided, into a distal and a proximal portion, the latter representing the inner metatarsal pad; the outer metatarsal pad is well developed, sharply defined, and about twice as long as wide.

In the foregoing genera the hind foot is larger in every way than the fore foot.

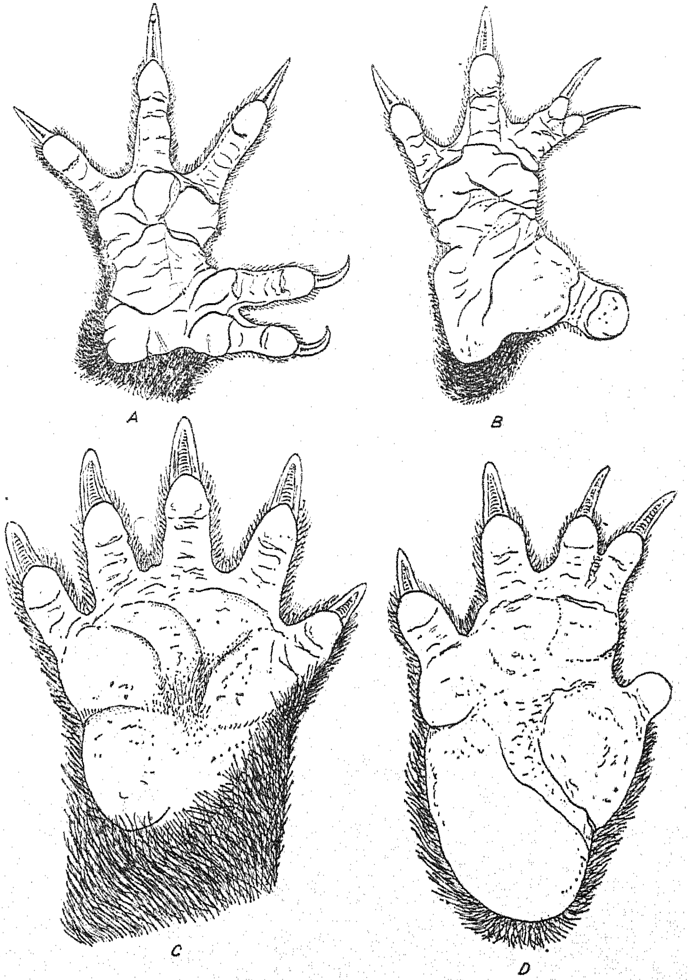
In *Phascolarctos* the hind foot is not larger than the fore foot. It differs from the hind foot of the other genera in having the united second and third digits relatively much longer and only a little shorter than the fourth; the lobes of the plantar pad are feebly differentiated, being fused to form a transverse cushion, with irregularly convex anterior and irregularly concave posterior border. The great pad of the hallux is undivided, and there is no distinctly defined external metatarsal pad. Thus in the development of the pads the foot of this genus differs more from that of *Pseudochirus* than from that of *Trichosurus*.

The hind foot of *Phascolomys*, as has often been pointed out, is a fossorial modification of the Phalangerine scansorial hind foot, resulting from the conversion of the sharp, curved claws of the latter into longer, stronger, and straighter claws, from the approximate equality in length between the fourth and the united second and third digits, the reduction in bulk of the great pad of the hallux so that it projects only slightly beyond the inner margin of the foot, with the terminal segment of the digit planted like a hemispherical tubercle upon it, and from the practical obliteration of the pads with expansion of the heel; but, as in the Phalangerine foot, the fifth digit is more widely separated from the fourth than the latter is from the third, although the digit in question is relatively shorter and the space above mentioned somewhat wider.

---

[*] These two united digits act as a fur-comb in Marsupials. Possibly they were primarily modified for that function. Generally they are too small in arboreal forms to be of much use for grasping. But this cannot be maintained in the case of *Phascolarctos*; and in *Phascolomys* they are large enough to be subservient to digging. But in the Kangaroos they appear to be retained solely for the purpose mentioned, and may frequently be seen to be so employed. Moreover, it is significant that these are the only digits in *Tarsipes* which have other than rudimentary claws.

Text-figure 25.



A, B. Right fore and hind foot of *Phascolarctos cinereus*.
C, D. „ „ *Phascolomys ursinus*.
× ½.

By their feet the genera may be distinguished as follows:—

- *a.* Feet fossorial with digits short, claws long, blunt and slightly curved, and the granular pads but little differentiated; hallux short, its distal phalange reduced to a button-like excrescence on the shortened lobe, which, however, still retains the capacity for movement in the opposable plane ... *Phascolomys.*
- *a'.* Feet scansorial and prehensile, with longer digits and sharp, curved claws, and differentiated pads; hallux very large and opposable, with well-developed terminal phalange.
  - *b.* Fore foot as large as hind foot, with comparatively long and narrow sole; the inner lobe of the plantar pad small and attached to the base of the second digit, which is separated by a long space from the third; the inner lobe of the carpal pad small, isolated from the outer and attached to the base of the first digit (pollex); second and third digits of hind foot comparatively large, strongly prehensile ..... *Phascolarctos.*
  - *b'.* Fore foot smaller than hind foot, with shorter, broader sole; the inner lobe of the plantar pad large, in contact, or nearly so, with the rest of the pad and fused into one mass with the inner lobe of the carpal pad, there being no differtiated pad at the base of the first digit (pollex); second and third digits of hind foot short, weakly prehensile.
    - *c.* A comparatively long space between the third and second digits of the fore foot, the second acting in unison with the first like a double opposable pollex; pads striated ... *Phalanger* and *Pseudochirus.*
    - *c'.* The five digits of the fore foot evenly spaced, the second in no respect opposable to the next, and the first or pollex only slightly so; pads granular................................ *Trichosurus.*

The Pouch.—I have seen no fresh female examples of *Phalanger* and *Pseudochirus.*

In *Trichosurus* the pouch, as in *Macropus*, is deeper than wide, its orifice has a well-developed lateral and posterior rim but no overhanging anterior rim; it therefore looks forwards *; and in the specimen examined there were only two teats, not four, as stated by Winge to be characteristic of the Phalangeridæ.

In *Phascolomys* the pouch is a little wider than long, being deeper laterally, especially anteriorly, than behind or mesially in front, and a little deeper behind than mesially in front, the muscular rim overhanging the cavity all round; and there is a single pair of teats.

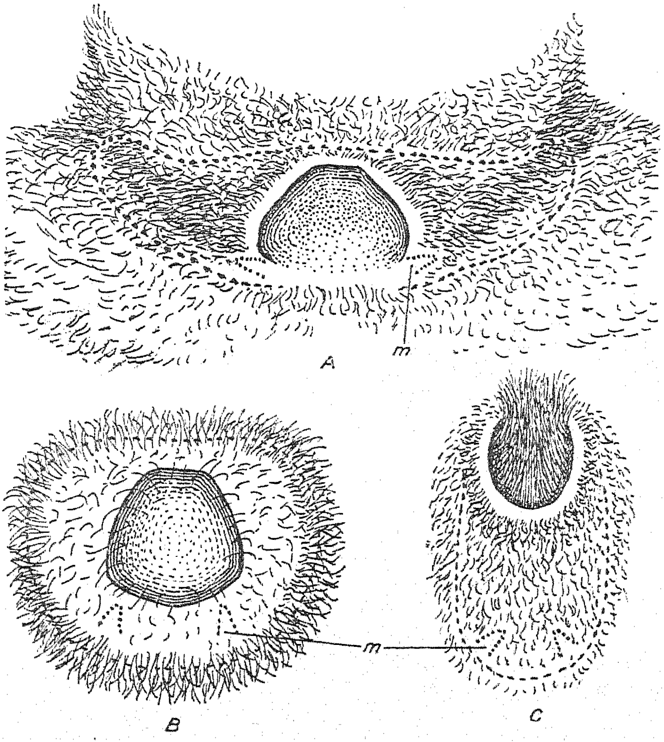
In *Phascolarctos* the pouch, as recorded by Forbes, is much wider than long, being extended, gradually narrowing as it goes, along the depression between the muscles of the thigh and abdomen nearly as far as the edge of the flap of integument joining the hind leg to the body, its width being about three times its length. The orifice looks slightly backwards, the muscular rim overhanging the cavity laterally and to a slight extent in the middle line in front, but ceasing on each side close to the position of the single teat. The orifice therefore looks backwards.

---

* In his volume on Marsupials (Allen's Naturalists' Library, p. 76, 1894), Lydekker wrongly states that the orifice of the pouch is directed backwards in Phalangeridæ.

From the description of these three pouches it is evident that the pouch of *Phascolomys* is structurally intermediate in many respects between those of *Trichosurus* and *Phascolarctos*. The differences between the pouches of the last two genera, considering that both are arboreal forms, is remarkable, especially in view of the theory that has been advanced that the anterior upward aspect of the orifice is an adaptation to arboreal life or to the more or less upright attitude assumed by such terrestrial bipedal forms as *Macropus*, and conversely that the posterior aspect of the orifice is an adaptation to the terrestrial life and quadrupedal gait of such genera as *Thylacinus* and *Sarcophilus*. This theory entirely breaks down in the case of *Phascolarctos*, perhaps the most specialized scansorial genus in the entire order.

Text figure 26.



A. Pouch of *Phascolarctos cinereus.*
B. „ *Phascolomys ursinus.*
C. „ *Trichosurus vulpecula.*

The extension of the pouch beneath the integument with the mammæ (*m*) at its posterior end shown diagrammatically with dotted lines.

The deep, backwardly directed pouch of *Trichosurus* seems so well adapted for the safe retention and carrying of the young up in the trees that its replacement by a laterally directed pouch with the orifice opening towards the tail, such as is seen in *Phascolarctos*, seems most unlikely. The use of the lateral extension for lodging the young carried by a mother who doubtless climbs at times head-downwards is easy to imagine, but the reason for the reversion of the orifice demanded by the theory of the descent of *Phascolarctos* from the Phalangerine stock is puzzling. The structure of the pouch alone supplies evidence that *Phascolarctos* is not closely related to any genus of the Phalangeridæ.

The characters of the three types of pouches above described may be summarized as follows:—

a. The orifice, not encircled behind, opening backwards and downwards; cavity of pouch extended laterally on each side along the depression between the thigh and the abdomen	*Phascolarctos*.
b. The orifice subcircular, surrounded by a flap of skin all round; cavity subcircular, a little deeper laterally than elsewhere	*Phascolomys*.
c. The orifice opening forwards, at the anterior end of the cavity, which is longer than wide	*Pseudochirus*, *Phalanger*, *Trichosurus*.

The Classification of existing Diprotodonts.

My opinion on the classification of the Diprotodonts is as follows:—

1. Winge's removal of *Phascolarctos* from the Phalangeridæ must be accepted. But although that genus shows points of resemblance to *Phascolomys* not shared by other existing Diprotodonts, the differences between them are too many and too important to admit of their ascription to the same family. Moreover, if we adopt as criteria of family rank such characters as those distinguishing the Kangaroos from the Phalangers, the characters separating the Koala and the Wombat should, I think, be given superfamily rank indicated by the titles Phascolarctoidea and Phascolomyoidea. Assuming Winge to have correctly placed the extinct forms above referred to, the Phascolarctoidea will contain the two families Phascolarctidæ (*Phascolarctos*) and Thylacoleonidæ (*Thylacoleo*); and the Phascolomyoidea the two families Phascolomyidæ (*Phascolomys, Lasiorhinus, Phascolonus*) and Diprotodontidæ (*Diprotodon, Nototherium*).

2. The two above-mentioned superfamily groups are individually equivalent to a group of that rank, containing the rest of the Diprotodonts, for which two names are available, Hypsiprymnoidea and Phalangeroidea. I prefer the latter on account of its greater familarity and its derivation from the name of a more primitive genus. Accepting for this group Thomas's families Macropodidæ and Phalangeridæ, it seems clear in the case of the former that if the characters of *Potorous* and its allies entitle

them to rank as a subfamily—and I see no reason for dissenting from that view,—the characters of *Hypsiprymnodon* must be given the higher rank of a family, the Hypsiprymnodontidæ equivalent to, and standing between, the Macropodidæ and the Phalangeridæ, but not definitely assignable to either.

From the typical Phalangeridæ constituting the subfamily Phalangerinæ, the genera *Pseudochirus* and *Petauroides*, characterized by the crescentic pattern of the molar teeth, may be separated as the Pseudochirinæ as proposed by Winge. But it does not appear to me that proper appreciation has been shown for the characters of the very highly specialized genus *Tarsipes* *, which differs profoundly from the Phalangeridæ in the structure of the skull, teeth, tongue, snout, and alimentary canal, as Thomas recorded. The genus seems to be at least as widely divergent from the Phalangeridæ as are the Macropodidæ. These two families, indeed, are linked by the Hypsiprymnodontidæ, and the evolutionary stages by which the Kangaroos have been derived from the Phalangerine stock may be traced with reasonable certainty through living forms. But all the hypothetical intermediate genera between *Tarsipes* and the Phalangers have died out, leaving that genus isolated. And since, in my opinion, it differs more from the typical Phalangers than do the Pseudochirines, it may be raised at least to the rank of a family—Tarsipedidæ.

Briefly, the existing genera of Diprotodonts may be classified as follows:—

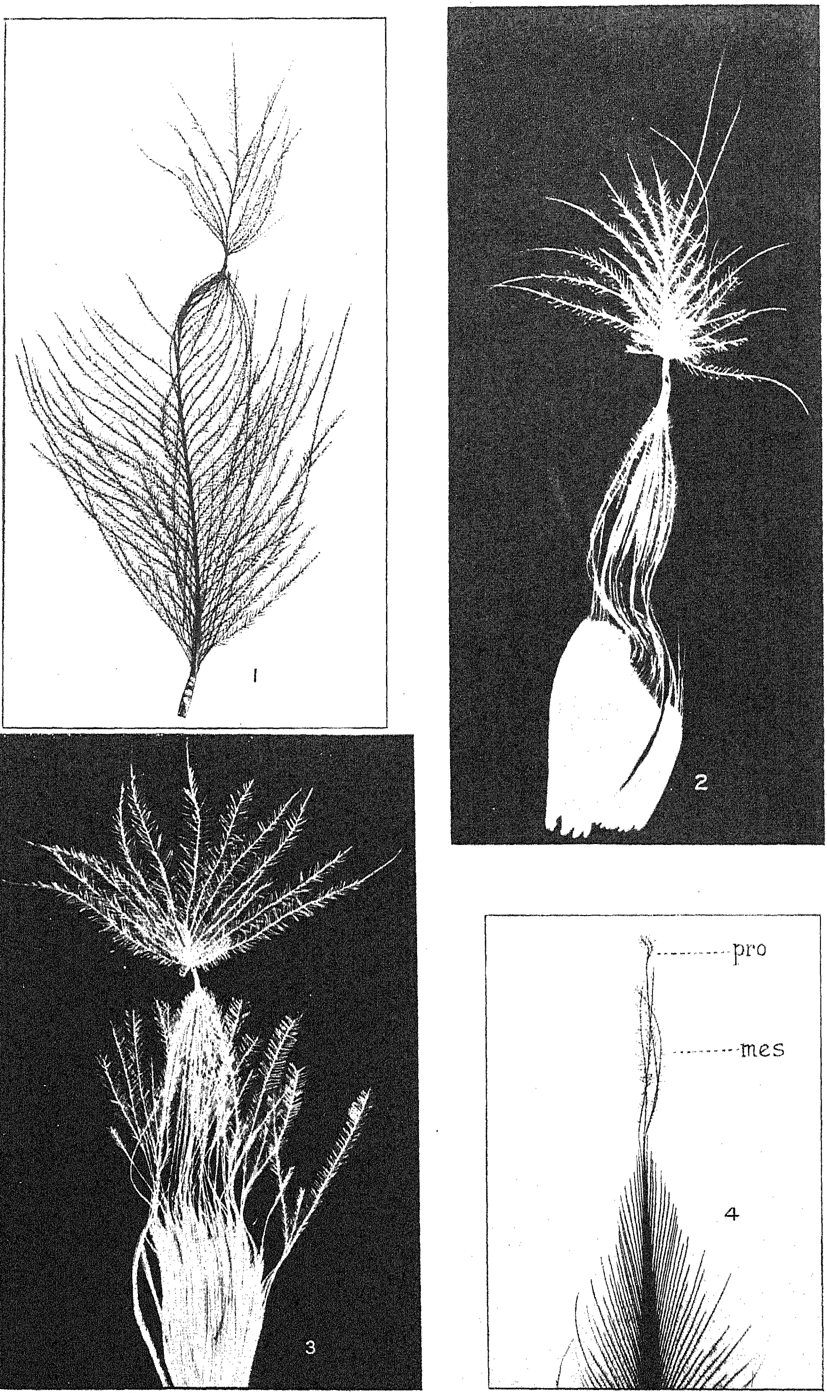
Phalangeroidea.
- Fam. MACROPODIDÆ.
  - Subfam. MACROPODINÆ.
  - ,, POTOROINÆ.
- Fam. HYPSIPRYMNODONTIDÆ.
- Fam. PHALANGERIDÆ.
  - Subfam. PHALANGERINÆ.
  - ,, PSEUDOCHIRINÆ.
- Fam. TARSIPEDIDÆ.

Phascolarctoidea.
- Fam. PHASCOLARCTIDÆ.

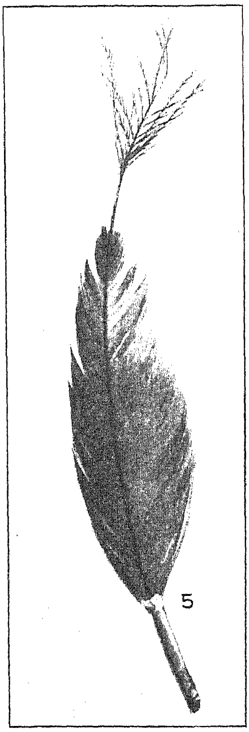
Phascolomyoidea.
- Fam. PHASCOLOMYIDÆ.

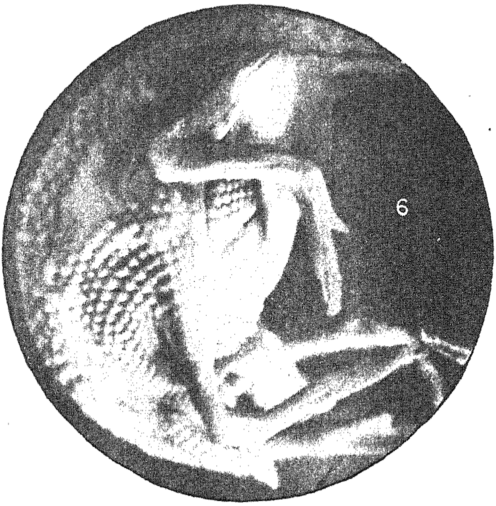
---

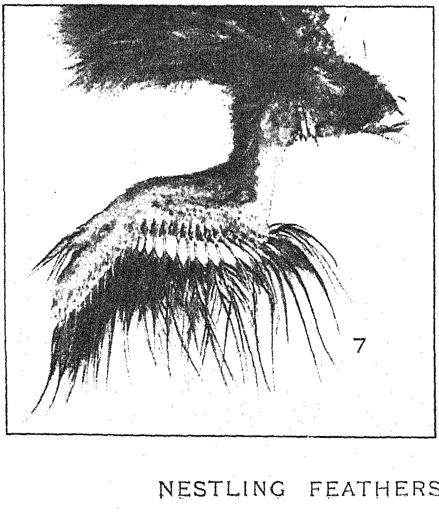
* Winge and Bensley even considered the characters of this genus to be of less systematic value than the concentric molars of *Pseudochirus*.

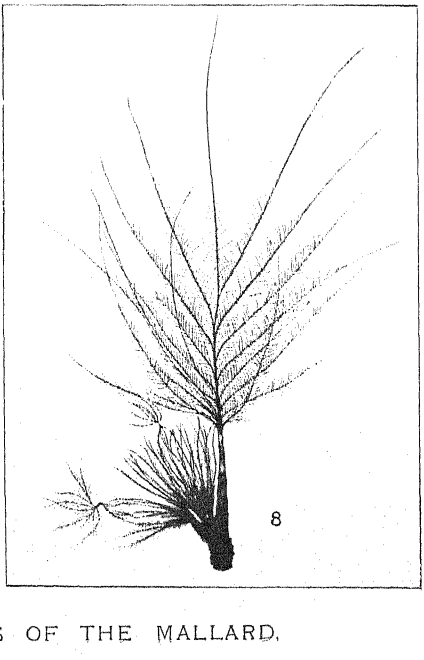


NESTLING FEATHERS OF THE MALLARD.

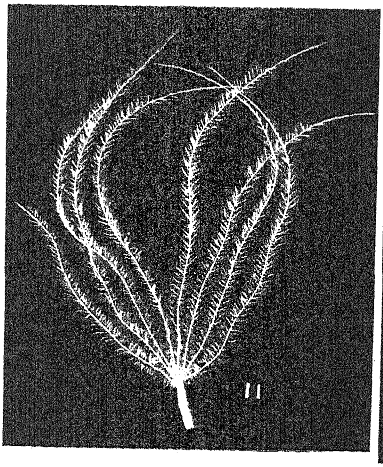


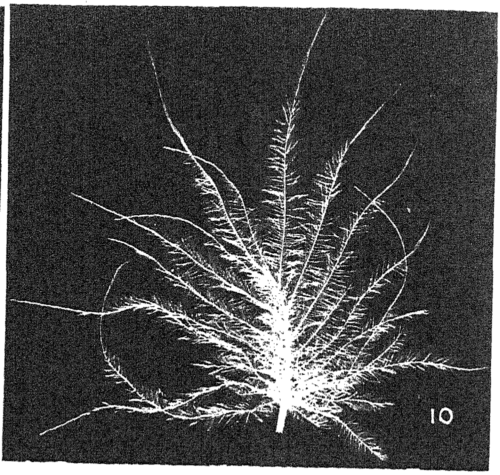


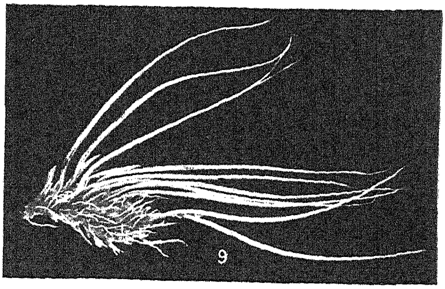


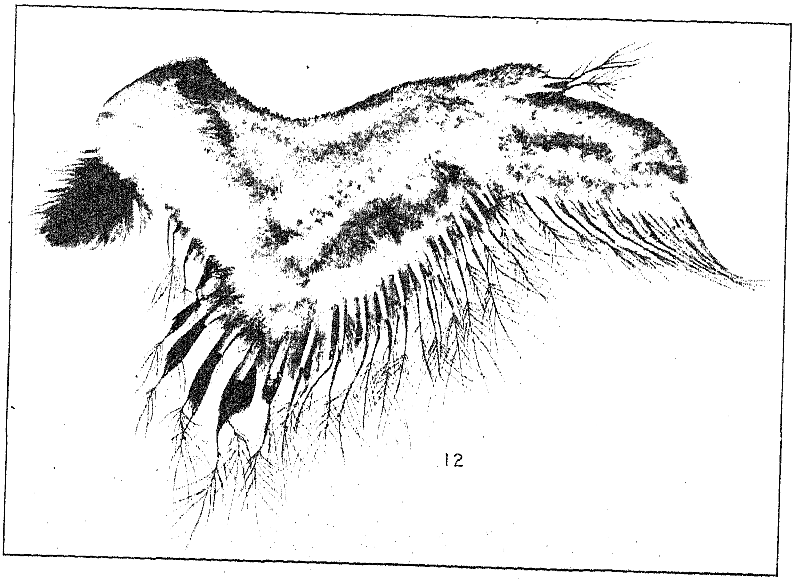


NESTLING FEATHERS OF THE MALLARD.

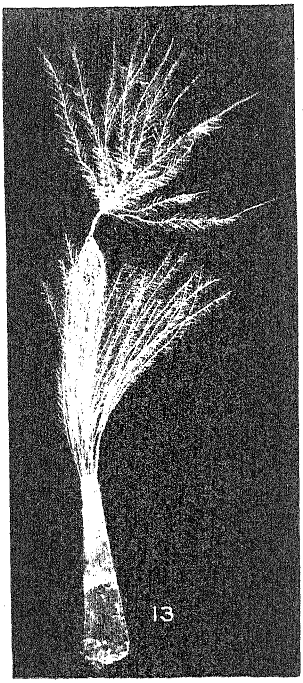


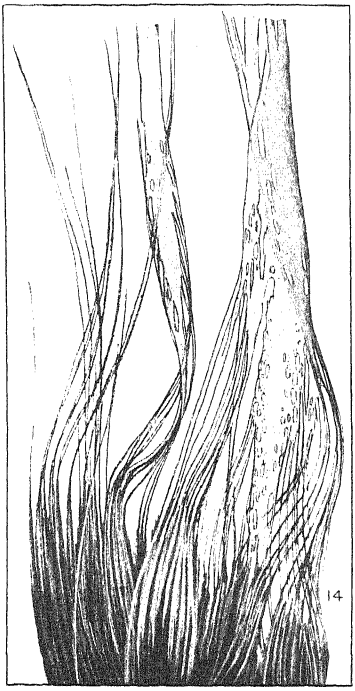


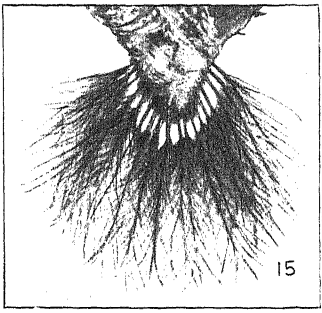


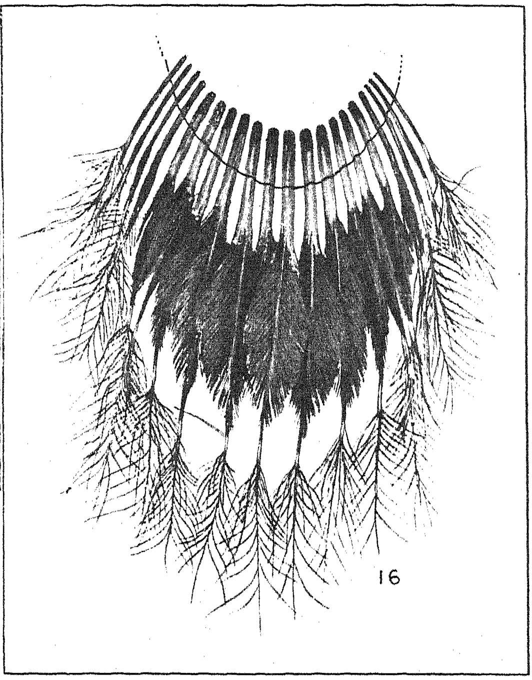


NESTLING FEATHERS OF THE MALLARD.

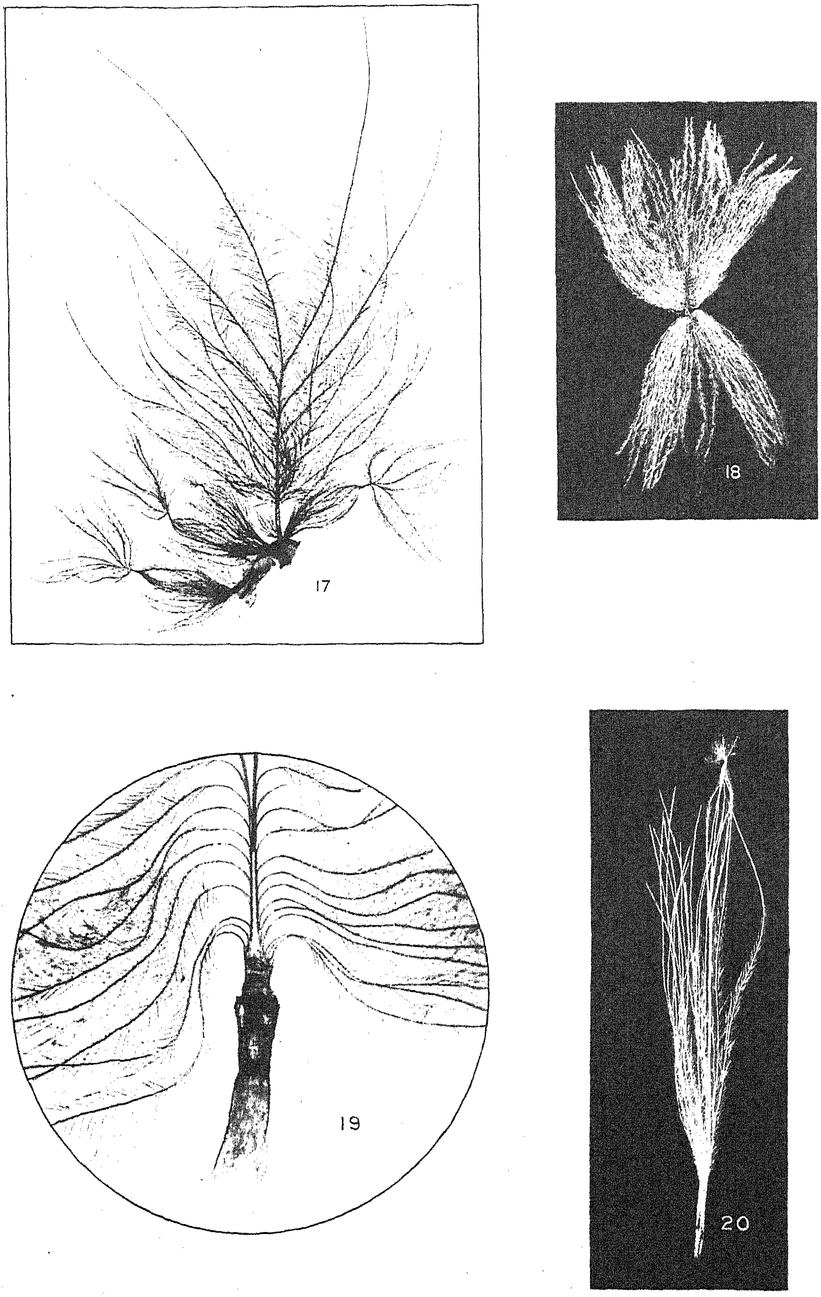

13


14

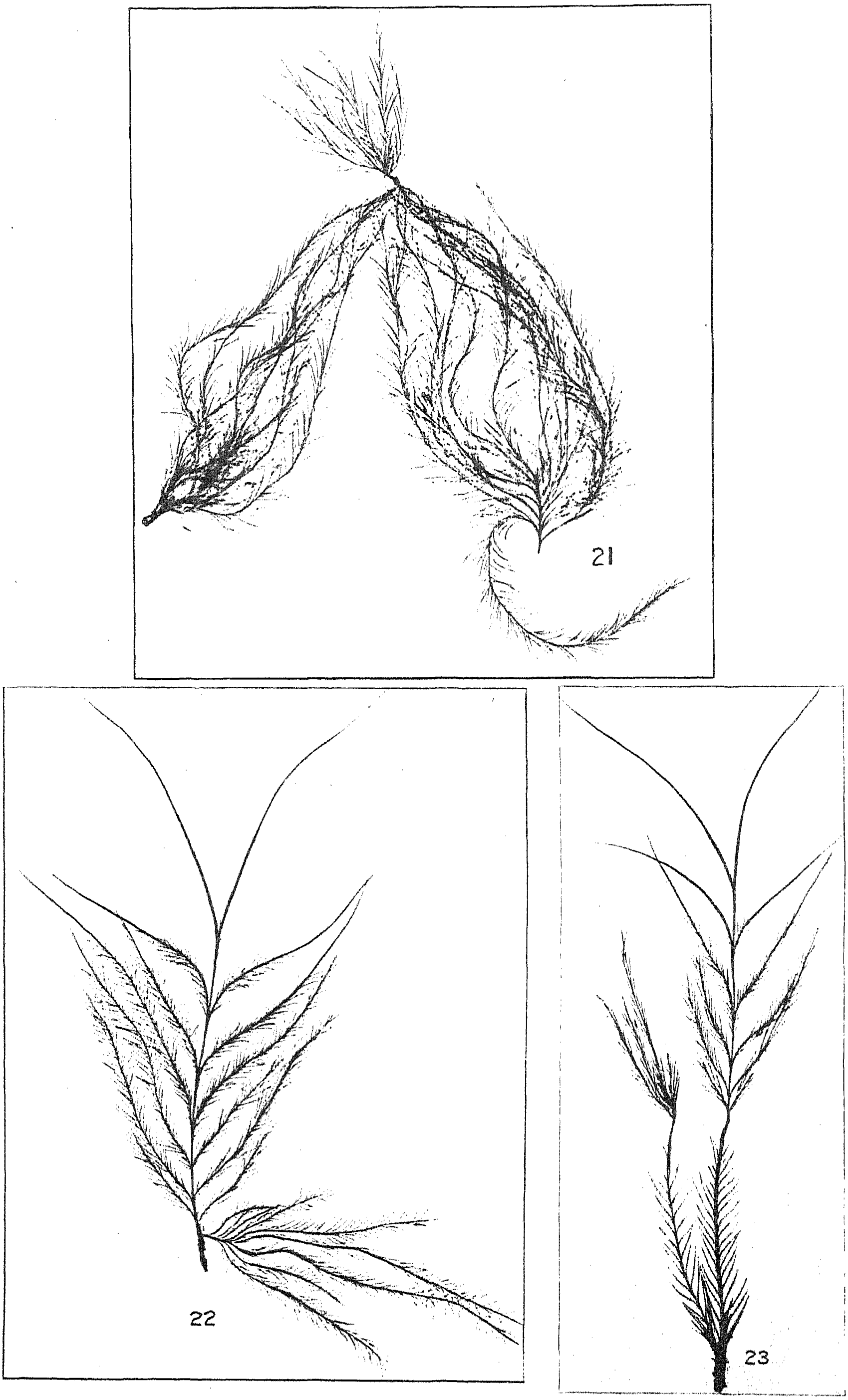

15


16

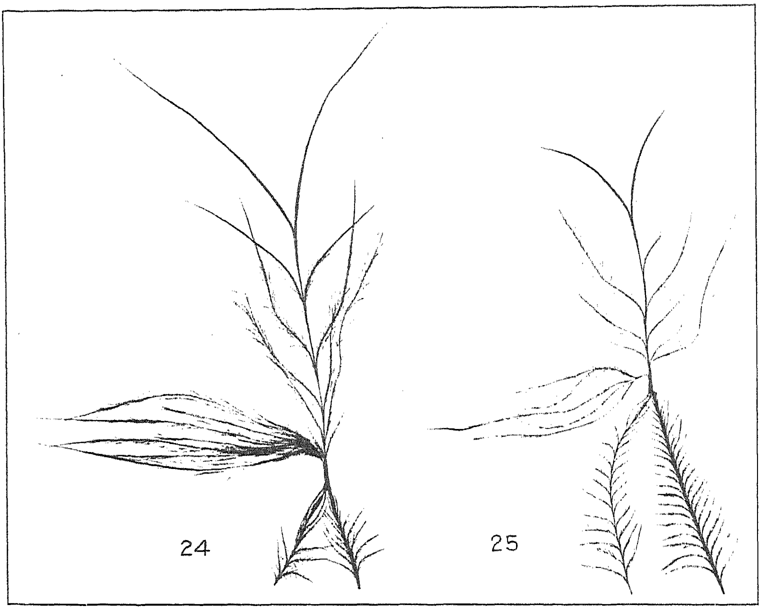
NESTLING FEATHERS OF THE MALLARD.

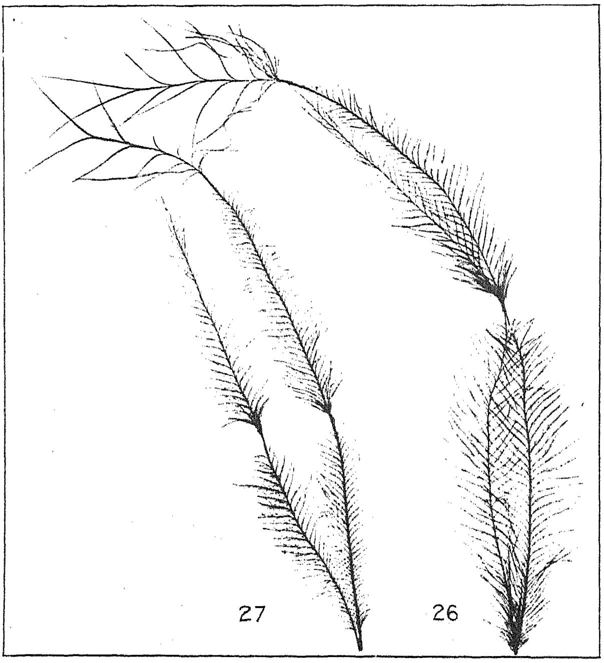


NESTLING FEATHERS OF THE MALLARD.

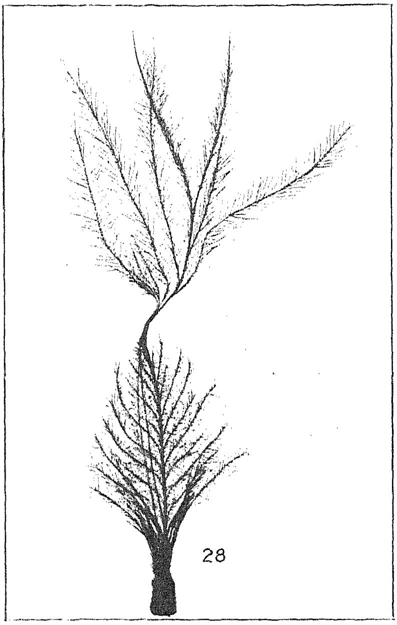


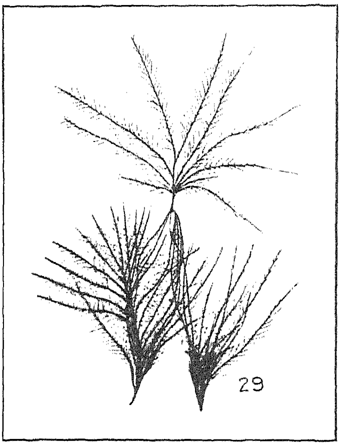
NESTLING FEATHERS OF THE MALLARD.

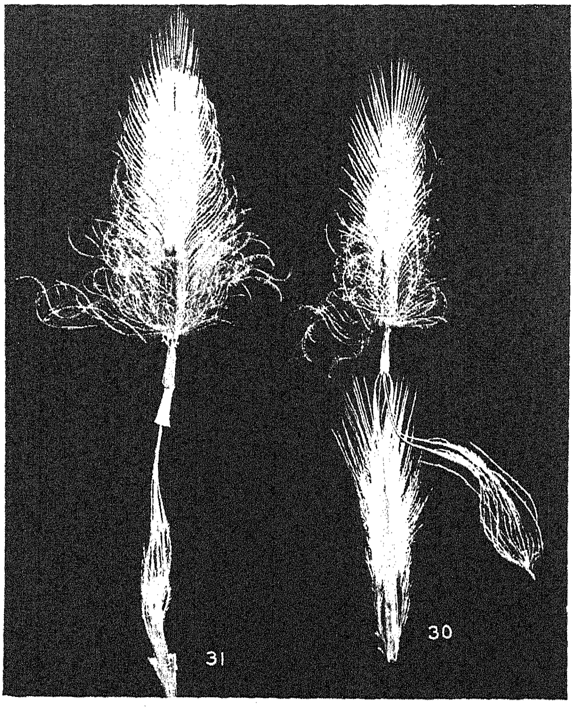




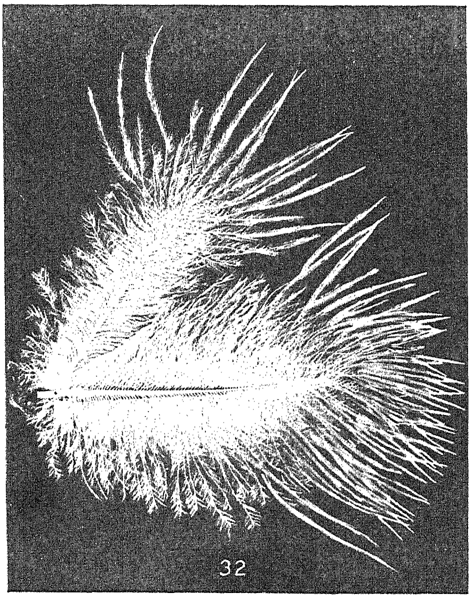
NESTLING FEATHERS OF THE MALLARD.

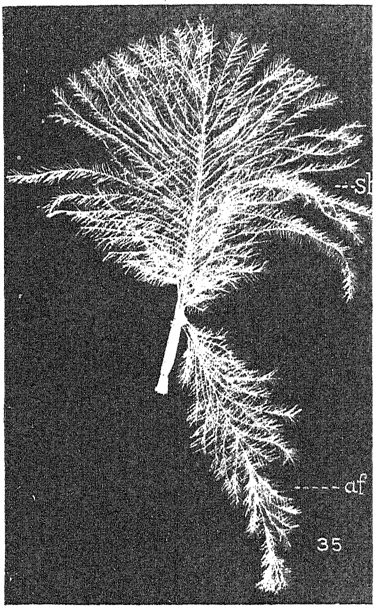

28

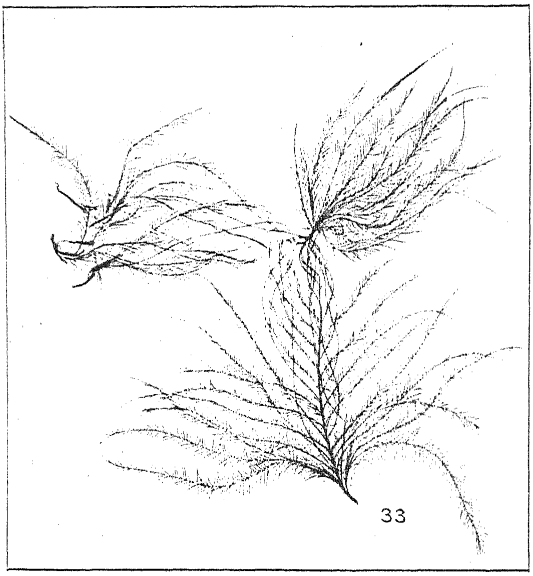

29

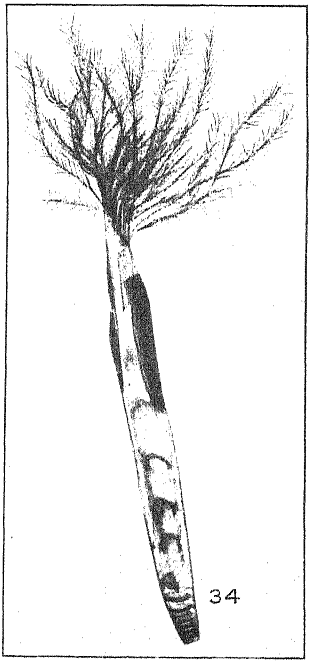

31 30

NESTLING FEATHERS OF THE MALLARD.

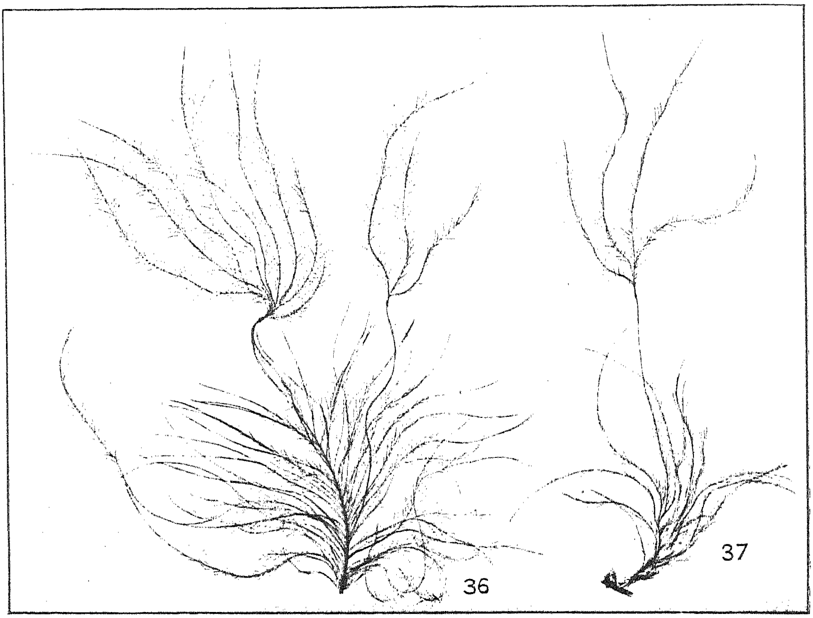






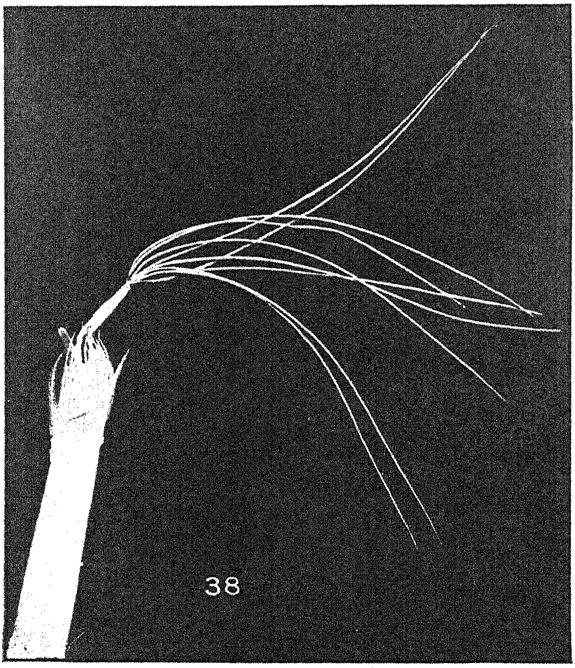


NESTLING FEATHERS OF THE MALLARD.



36

37



38

NESTLING FEATHERS OF THE MALLARD.

34. The Nestling Feathers of the Mallard, with Observations on the Composition, Origin, and History of Feathers.

By J. Cossar Ewart, M.D., F.R.S., F.Z.S., Regius Professor of Natural History, University of Edinburgh.

[Received March 7, 1921: Read March 22, 1921.]

(Plates I.–X.; Text-figures 1–14.)

I. The Nestling Feathers of the Mallard (*Anas boscas*).

In a recent paper in 'The Ibis' it is pointed out that "there is no branch of ornithology that has remained so long neglected as the study of nestling birds, nor is there one in which so many problems await solution" (**1**). That the study of nestling feathers has been neglected will be admitted when it is mentioned that up to 1906 it was not realized that the true feathers (pennæ) may be preceded by two generations of nestling feathers (prepennæ), that ornithologists have not yet made up their minds whether the familiar coat worn by newly-hatched chicks and ducklings corresponds to the first (protoptile) or to the second (mesoptile) nestling coat of Penguins, and that morphologists have not yet ascertained whether nestling and other feathers originally consisted of one shaft or of two complete shafts like the nestling and adult feathers of the Emu.

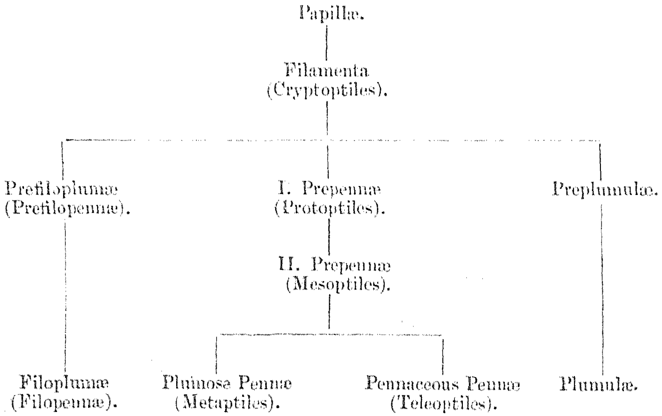
True or definitive feathers vary greatly in size and structure; nevertheless, they may be said to belong either to a plumose (metaptile) or to a pennaceous (teleoptile) type. The plumose true feathers are characterized by barbules which may possess cilia but never have hooklets (hamuli); in pennaceous feathers some of the barbules are armed with hooklets, by means of which the barbs are "woven" into a web—in the wing-quills of flying birds we have highly specialized teleoptiles; in the plumose feather from a Mallard represented in Pl. I. fig. 1 we have an example of a simple metaptile, bearing a protoptile.

In Penguins all the true feathers are probably preceded by both protoptiles and mesoptiles (text-fig. 3), but in many birds there is only one nestling coat—the mesoptiles have either been completely suppressed or are represented by inconspicuous and barely recognizable vestiges.

In most birds there are numerous hair-like feathers associated with, and intimately related to, the true feathers. As these hair-like feathers are preceded by minute prepennæ—are, in fact, degenerate pennæ,—they might be known as filopennæ.

Further, in many birds there appear between the true or contour feathers (pennæ) true down feathers (plumulæ). In all the Ducks, Geese, and Penguins examined the plumulæ are preceded by preplumulæ.

The relation of the various kinds of feathers of mature birds to nestling feathers is indicated in the following table:—



1. *The Prepennæ.*

The most concise and authoritative statement I have come across about nestling feathers occurs in 'Newton's Dictionary of Birds.' It is there stated that neossoptiles (*i. e.* protoptiles) "are characterized by (1) a very short calamus, (2) an insignificant or ill-defined rhachis—if there be one at all, (3) the almost universal absence of cilia, (4) long and slender rami (barbs), and (5) the absence of an aftershaft except in Dromæus"; in another paragraph it is stated that the barbules (radii) of the aftershaft have no cilia (2). A more recent statement about neossoptiles is that the feathers forming the familiar coat of newly hatched ducklings and chicks are not protoptiles but mesoptiles, and hence correspond to the feathers forming the long fur-like second coat of Penguins (3).

I may at once state that in Mallard ducklings the outer nestling coat consists of typical protoptiles characterized by (1) a well-developed calamus which may contain over twenty "cones," (2) a well-developed rhachis, (3) well-developed and in some cases hook-like cilia, (4) short stiff, as well as long slender barbs, and (5) by a well-developed aftershaft, the barbules of which bear cilia.

In ducklings the protoptiles vary in size—some are over 30 mm. in length and resemble plumose (metaptile) feathers, others are under 10 mm. in length and resemble preplumulæ. But the small as well as the large protoptiles consist of a calamus, a shaft, and an aftershaft. In addition to assisting the preplumulæ, and later the plumulæ, in diminishing the flow of heat from the skin, the protoptiles, as a rule, prevent water reaching the under coat of true down; by the pigment they contain they help to make the duckling inconspicuous.

(1) *The Wing-Quill Protoptiles.*

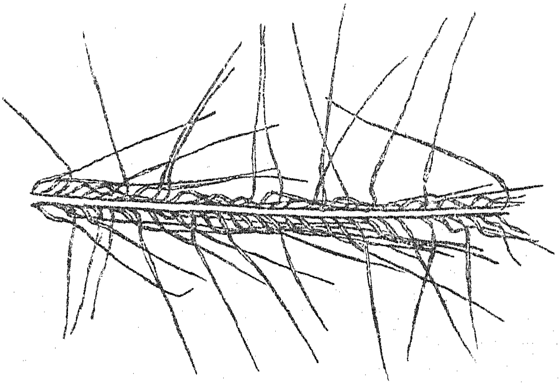
Though Ducks have been living under domestication for well-nigh two thousand years, their nestling feathers have apparently never been systematically examined. That no serious attempt has been made to study the nestling feathers of ducks and other Anseres, and of fowls and other Galli, is made evident by a perusal of Mr. Pycraft's important monograph on the Emperor and Adélie Penguins. In an interesting chapter on the composition and sequences of the neossoptiles, after pointing out that "the penguin must certainly be regarded as having preserved what must be looked upon as a somewhat, perhaps very, ancient succession of plumages," Mr. Pycraft states that "in the light of my recent discovery" it is clear that the "down" feathers of the Galli and Anseres "do not, as I imagined, represent a primitive type of down feather homologous with the woolly, and so presumably degenerate down of say the Alcidæ, but answer to mesoptyles. The protoptyle or first generation of feathers would seem to be wanting in these birds, but I had the good fortune to discover small tufts of down adhering to the tips of the mesoptyles of a young *Chloëphaga rubidiceps*. Thus we may assume that this first generation, since it has not yet been traced, has been lost in all the Galli, and probably all the Anseres save perhaps this species and one or two allied genera" (**3**).

As Pl. I. figs. 2 & 3 show, I have succeeded in tracing two generations of nestling feathers in the Indian Runner Duck and in the common Domestic Goose, and thereby have proved that the coat worn by newly-hatched Ducks and Geese consists of protoptiles corresponding to the first or protoptile nestling coat of Penguins. In the case of the King Penguin the first or protoptile coat is apparently in the act of disappearing; but in all the Anseres and Galli I have examined it is the second coat that has been lost or is in the act of disappearing. Though in the wings of some Ducks and Geese well-developed mesoptiles still make their appearance, the tail-quill mesoptiles are either vestigial or have been completely suppressed. That the protoptile is in the act of disappearing in the tail of the Penguin is suggested by Pl. I. fig. 4, while Pl. II. fig. 5 clearly indicates that as the mesoptile was suppressed in the tail of the Mallard the protoptile was enlarged.

With the help of a prematurely developed "nestling tail" the Mallard duckling begins to dive at the end of the second week, but, owing to the development of the wings being retarded, flying only becomes possible at the end of the eighth week. That the development of the wing is from the outset retarded is suggested by Pl. II. fig. 6, a ten days' duck embryo. In this embryo the papillæ which develop into the tail-quill protoptiles are large, but the wing-quill papillæ are only beginning to make their appearance*.

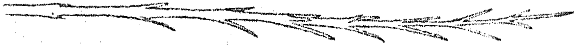
In a five weeks' duckling some of the tail-quills measure 50 mm., but the wing-quill rudiments at the end of the fifth week only measure 4 mm. The wing of a twenty-five days' Mallard is represented in Pl. II. fig. 7, natural size, and the protoptile of a secondary wing-quill of a thirty-eight days' Mallard in Pl. II. fig. 8. Though the wing-papillæ appear late they soon develop into filaments—filaments of a thirteen days' Mallard embryo are represented in Pl. III. fig. 9. With the exception of the calamus the development of the protoptile is, as a rule, completed before the end of the twenty-eighth day of incubation, so that the vascular pulp—which made the development of the nestling feather possible—may be converted into bloodless pith before hatching. Even when the duckling escapes from the shell the nestling coat consists of bristle-like filaments. But as the duckling dries, the thin friable sheaths which protected the protoptiles during development disintegrate, with the result that the protoptiles expand and provide the duckling with a wonderfully complete outer nestling coat. A wing-quill

Text-figure 1.



Part of a barb from the shaft of a protoptile of a 16 days' duckling showing barbules spirally twisted at their origin. × 25 dia.

Text-figure 2.



Distal part of a barbule of a protoptile of a 23 days' duckling showing cilia. × 250 dia.

---

* It is conceivable that there is some relation between the slow development of the wing and the persistence of wing-quill mesoptiles.

protoptile of a twenty-six days' duck embryo artificially removed from a filament (like the long filaments in Pl. III. fig. 9) is represented in Pl. III. fig. 10.

The wing-quill protoptiles are complete feathers: *i. e.*, each consists of a calamus, a shaft, and an aftershaft. The calamus, *though only 3 or 4 mm. in length*, is well *formed*, contains several "cones," and remains intact until the protoptile is shed—in Penguins the part of the epidermic tube which represents a "calamus" usually soon splits, with the result that the individual protoptile barbs are directly continuous with mesoptile barbs (text-fig. 14). Though the growth of the shaft and aftershaft is arrested before hatching, the calamus may continue to grow after hatching.

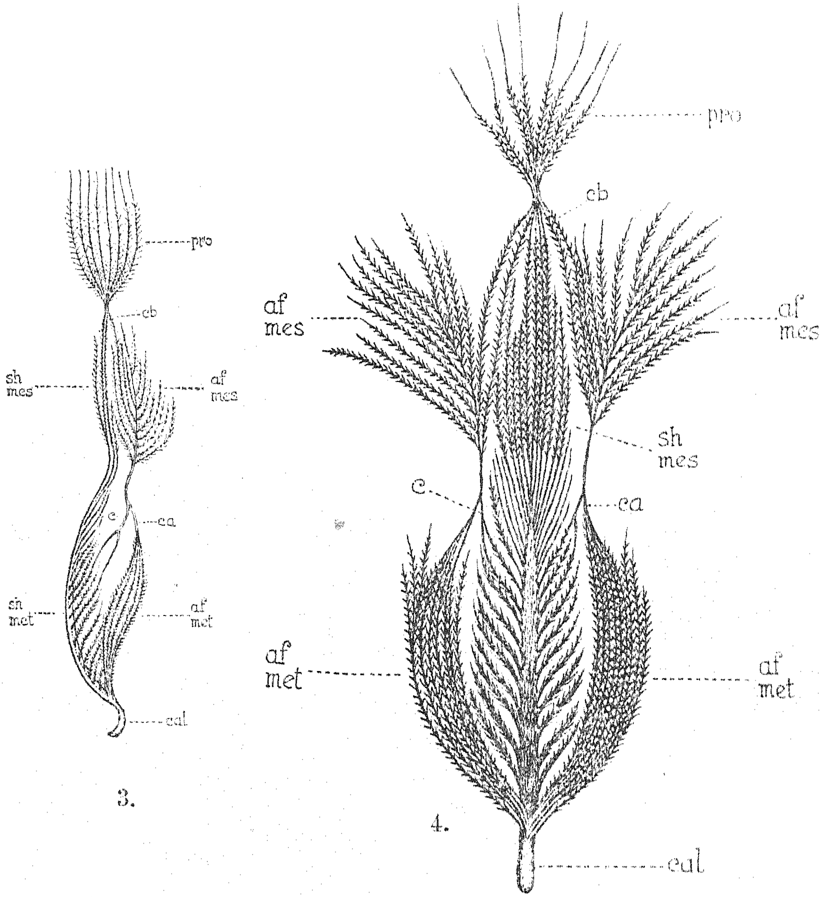
The shaft is made up of a rhachis, continuous with the outer segment of the calamus, and usually of seven or eight pairs of barbs, which vary in length and in the number of barbules they possess. The two terminal barbs (which by uniting formed the distal part of the rhachis) end in long slender processes destitute of barbules. The aftershaft (Pl. III. fig. 11), continuous with the inner segment of the calamus, usually consists of eight barbs bearing barbules. Sometimes the four mesial barbs of the aftershafts unite to form a short rhachis. The barbules of the shaft are spirally twisted at their origin (text-fig. 1), but the aftershaft-barbules only curve slightly on leaving the barb. It has frequently been stated that aftershaft-barbules of true as well as nestling feathers have no cilia, but cilia are invariably present on the barbules of the protoptile aftershaft of Mallard ducklings. Part of a barbule with cilia is given in text-fig. 2.

The wing-quill protoptiles may all be present at the end of the sixth week (Pl. III. fig. 12), but some of them have usually been shed before the end of the seventh week. Though Mallards begin to fly during the ninth week, the development of some of the wing-quills is only completed during the tenth week.

(2) *The Wing-Quill Mesoptiles.*

Up to 1906, as already mentioned, it had not occurred to ornithologists that true feathers (pennæ) might be preceded by two generations of nestling feathers (prepennæ), and mesoptiles have apparently not yet been recorded in connection with wing-quills.

Early in the century two National Antarctic Expeditions were fortunate enough to collect material which made possible a fairly exhaustive study of the development and history of the nestling feathers of Penguins. The penguin material brought home by the English National Antarctic Expedition was reported on by Mr. Pycraft; that collected by the Scottish National Antarctic Expedition by Dr. Eagle Clarke. In a paper published in 1906 in 'The Ibis,' Dr. Clarke announced that he had discovered two coats of nestling feathers in the Ringed and Gentoo Penguins, Text-figures 3 & 4.



Diagrams indicating the relation of the mesoptile to the protoptile and to the first true feather of a Ringed Penguin:—*pro.*, the protoptile, consisting of four outer barbs representing a shaft and of four inner barbs representing an aftershaft. *sh.mes.*, shaft of mesoptile continuous distally with protoptile and proximally with the shaft of the true feather. *af.mes.*, mesoptile aftershaft also continuous with the protoptile and the true feather. *cb.*, connection with protoptile. *c.*, connection with shaft of true feather. *ca.*, connection with aftershaft of true feather. *cal.*, calamus.

and in the following year an important paper by Mr. Pycraft on the Emperor and Adélie Penguins was published which deals with the composition and sequences as well as with the structure of nestling feathers.

Dr. Clarke refrained from stating whether the silky-white protoptile coat, or the grey fur-like mesoptile coat, of the Ringed Penguin, corresponds to the nestling coat worn by newly-hatched chicks and ducklings. But Mr. Pycraft, in discussing the sequences of nestling-feathers, states that there are good reasons for assuming that in most of our common birds the first or protoptile coat has been lost, and adds that the feathers forming the adult coat of the Emu might possibly consist of mesoptiles.

Whether ornithologists have, as a rule, adopted Mr. Pycraft's views it is impossible to say, but it may be mentioned that Mr. Ingram, in the 'Ibis' paper already referred to, points out that a study of the nestling plumage of the Raptores suggests that in some cases, at any rate, it is the second and not the first generation of nestling "down" that has been suppressed (**1**).

When, some years ago, I was led to study the feathers of Penguins, I assumed that birds with only one nestling coat had lost the first or protoptile coat; but the examination of a number of nestlings soon made it evident that when in the Galli and Anseres there is only one generation of nestling feathers, it is owing, not to the absence of the protoptiles, but to the suppression of the mesoptiles.

In the account of the nestling feathers of the Emperor Penguin, Pycraft states that the mesoptiles are umbelliform, and that in the Adélie Penguin the mesoptile is in part attached to the main shaft, but mainly to the aftershaft. I have not had an opportunity of studying the nestling feathers of either the Emperor or Adélie Penguins, but from material placed at my disposal by Dr. Eagle Clarke I have worked out the structure of the mesoptiles of the Ringed Penguin. In this species the mesoptile is extremely complex: it consists (1) of an outer small series of barbs, which extends between the protoptile and the tip of the true feather, and hence occupies the position of, and doubtless represents, a shaft; and (2) of an inner series of barbs (text-fig. 3), arranged to form two or three bundles, which as obviously represent an aftershaft. The chief connections of the mesoptile in the Ringed Penguin are diagrammatically represented in text-fig. 4, which indicates that the mesoptile consists of a simple shaft extending between the protoptile and the tip of the true feather, and a complex aftershaft connected with the shaft as well as with the aftershaft of the true feather.

In a Mallard duckling at the end of the fifth week the mesoptile looks as if it would develop into a simple umbel not unlike the umbelliform protoptiles of Penguins. But this appearance is due to the fact that nestling feathers, like true feathers, are developed, not out of a scale-like plate, but out of an epidermic tube surrounding a highly-vascular dermic pulp and

Text-figure 5.

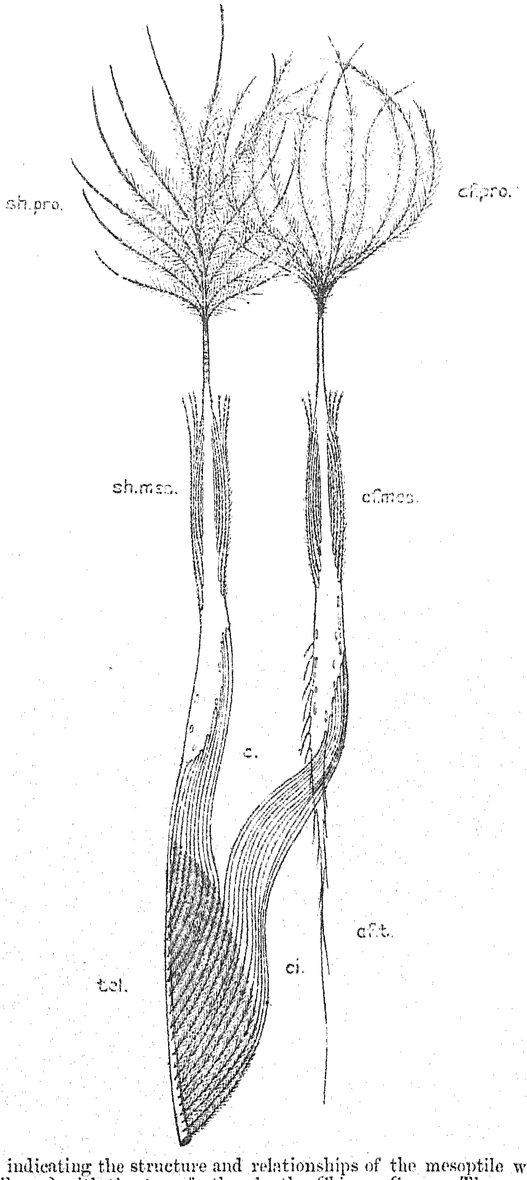


Diagram indicating the structure and relationships of the mesoptile with the protoptile and with the true feather in the Chinese Goose. The mesoptile shaft (*sh.mes.*), which lies between the protoptile shaft (*sh.pro.*) and the tip of a true feather, consists of numerous barbs and of a band representing a rhachis. Continuous with the rhachis is a perforated band from which slender cords (*c.*) proceed to the barbs forming the tip of the true feather (*tel.*). The mesoptile aftershaft is also continuous with a perforated band which ends in a vestige of an aftershaft of the true feather (*af.t.*). From the perforated band slender cords (*c* 1) proceed to barbs near the tip of the true feather. It will be observed that the aftershaft of the protoptile consists of twelve well-developed barbs armed with numerous barbules.

protected by a thin epidermic sheath. When the development is carried further, it becomes evident that in the Mallard the mesoptile consists of two sets of fibres, an outer set representing a shaft, and an inner, an aftershaft, each provided with a more or less distinct rhachis. Though the mesoptiles in Ducks may reach a considerable size, it is easier to make out their development and structure in Geese. The wing-quill mesoptiles, though well-developed in the Mallard, are not present in the Emden goose but as Pl. I. fig. 3 shows, the major wing-covert mesoptiles may reach a considerable size in Geese.

To start with, the mesoptile of a Chinese gosling looks as if it possessed a calamus (Pl. IV. fig. 13); the mesoptile barbs seem to proceed from a tube lying immediately in front of the tip of the true feather. That this tubular part represents a calamus is supported by the fact that it contains several "cones," but against the view that it is a true calamus is the fact that it is in the act of splitting longitudinally into numerous slender cords. In mesoptiles from older goslings part of the tubular portion is represented by two perforated bands, from which proceed numerous slender cords towards the wing-covert. Sometimes the mesoptile in goslings splits into two portions (Pl. IV. fig. 14, & text-fig. 5), an outer (the shaft) extending between the shaft of the protoptile and the tip of the wing-quill, and an inner (the aftershaft) extending between the protoptile aftershaft and the vestigial aftershaft of the wing-quill.

It may be mentioned that in the Anseres the mesoptiles vary greatly in structure—the proximal part of the aftershaft may be perforated and assume the form of a section of a relatively large tube (Pl. IV. fig. 14), or, like the rhachis of the shaft, be represented by a simple narrow band. Though in the Mallard and Chinese goslings the aftershaft, as well as the shaft of the mesoptile, has usually a distinct rhachis, in Emden goslings the whole of the mesoptile, as Pl. I. fig. 3 suggests, usually consists of simple barbs, one or two of which are continuous with the rhachis of the wing-covert shaft, while two or more end in a vestigial aftershaft. The barbules of the mesoptile, like those of the protoptile aftershaft, are narrow and provided with well-developed cilia. In the Ringed Penguin the mesoptiles closely agree in structure, but in the Ducks and Geese examined no two mesoptiles were alike in structure. The mesoptile coat is probably as useful now to Penguin chicks hatched within or near the Antarctic Circle as it was when originally acquired, during perhaps a cold phase of a glacial epoch. In the Anseres, though the protoptile coat still plays an important part, the mesoptile coat probably no longer counts in the struggle for existence. If this is the case there is no difficulty in accounting for its being well-developed in some parts but entirely absent in others, and for the marked variation amongst the mesoptiles which still persist.

The Mallard has wing-covert, as well as wing-quill, mesoptiles. The mesoptiles which precede the wing-coverts in the Mallard are especially interesting, because they indicate how the suppression of the mesoptiles was gradually accomplished. In the case of the disappearing protoptiles of the King Penguin (Pl. I. fig. 4) the size is gradually reduced until they are smaller than the minute bunch of barbs which precede the filoplumes of ducklings. In the case of the vanishing mesoptiles two sets of factors are evidently at work; one set arrests the development of the mesoptile barbs, another set accelerates the development of the barbs of the true feather, with the result that in course of time the tip of the true feather is found projecting into the base of the protoptile calamus.

Though in most cases the mesoptiles are gradually reduced in size, in some cases the length is maintained and either a few barbs with barbules are developed, or the simple epidermic tube splits into two or more bands, which for a time connect the protoptile to the tip of the true feather.

It may be mentioned that though all the wing-quill protoptiles and mesoptiles may be present in the Mallard duckling at the end of the sixth week (Pl. III. fig. 12), some of the mesoptiles are usually shed before the end of the seventh week, and all are usually lost before the middle of the eighth week. But though the wing-quills lose all their nestling feathers during the eighth week, some of the feathers of the humeral track may retain protoptiles and mesoptiles to the end of the eleventh week. The existence of the wing-quill mesoptiles in the Mallard proves conclusively that the nestling coat worn by newly-hatched Ducks and Geese corresponds, not as Pycraft suggested to the second generation of prepennæ in Penguins, but to the first or protoptile generation.

(3) *The Tail-Quill Protoptiles.*

The tail varies greatly in young aquatic birds. In Penguins the tail protoptiles have almost disappeared and the mesoptiles are only represented by a few simple barbs (Pl. I. fig. 4). In the Mallard the mesoptiles of sixteen of the eighteen tail-quills have completely disappeared, but the protoptiles of all the eighteen quills are larger and more complex than in the plumose (metaptile) feather represented in Pl. I. fig. 1. In Penguins steps are soon taken to develop the tail-quills with a view to their forming with the hind limbs a tripod useful in maintaining the erect attitude. In the Mallard the protoptiles form a "nestling tail" which plays an important part during the earlier portion of the period that Mallard ducklings behave like diving ducks*.

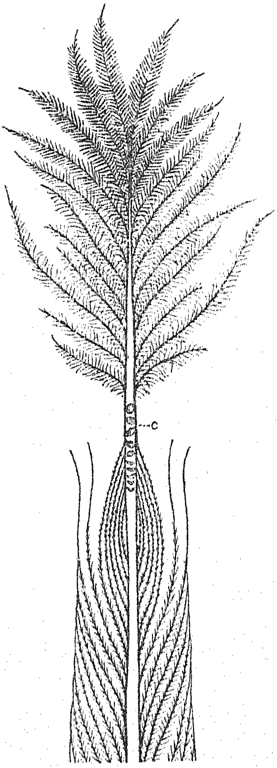
In a ten days' duck embryo the tail-quill papillæ † are easily identified (Pl. II. fig. 6), and by the twenty-fifth day of incubation they have grown into long filaments out of which escape immediately after hatching highly specialized protoptiles. During the first week the nestling tail consists only of protoptiles (Pl. IV. fig. 15), but during the second week the protoptiles are pushed from the skin by the tail-quills, or by vestigial mesoptiles. At the end of the fourth week the tail-quills may be nearly an inch in length, and they are still longer at the middle of the fifth week (Pl. IV. fig. 16). During the latter part of the fifth week the protoptiles begin to break off, and with the exception of the ninth from the middle line at each side, they are usually all shed by the middle of the sixth week.

---

* The adult Mallard, Mr. G. J. Millais informs me, "hardly ever dives except when in play during the love chase, or to escape when wounded."

† There are twenty tail-quill papillæ, but only eighteen of them develop into feathers large enough to rank as tail-quills. A paper "On the development of the Feathers of the Duck during the Incubation Period" was recently communicated to the Royal Society of Edinburgh by Augusta Lamont, B.Sc.

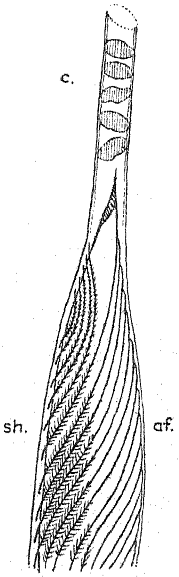
Text-figure 6.



This drawing shows that the rhachis of the shaft of a typical tail-quill protoptile ends in a calamus containing "cones," that this calamus is directly continuous with the expanded distal portion of the tail-quill rhachis, and that the connection of the protoptile with the teleoptile is strengthened by barbs at the tip of the tail-quill ending in the proximal portion of the protoptile calamus.

The calamus of the protoptiles is strong and rigid and firmly fixed to the expanded tip of the tail-quill rhachis. By way of strengthening the connection between the protoptile and the tail-quill, four or more pairs of the terminal barbs of the tail-quill are attached to the protoptile calamus (text-fig. 6). At the end of the second week the "nestling" tail and the other structures concerned are sufficiently developed to admit of young Mallards obtaining the greater part of their food by diving*. Notwithstanding the loss of the protoptiles during the sixth week, young Mallards usually continue to behave like diving ducks up to the end of the eighth week. From what has been said it is evident that the "nestling tail" of the Mallard duckling is not from first to last entirely composed of nestling feathers. It is a true nestling tail up to the middle of the second week, but from the

Text-figure 7.



The proximal portion of the calamus of a tail-quill protoptile containing "cones." As the calamus approaches the tip of the tail-quill it splits into an outer portion continuous with the expanded rhachis of the quill and a more slender inner portion continuous with a vestigial tail-quill aftershaft. *c.*, protoptile calamus with "cones." *sh.*, tail-quill shaft. *af.*, vestige of tail-quill aftershaft.

---

* Two of nine Mallard ducklings I had under observation began to dive on the thirteenth day: they were all diving on the fourteenth day.

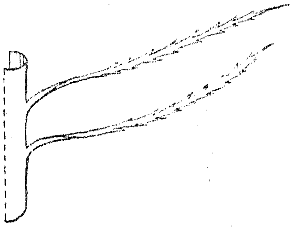
beginning of the third to the end of the fifth week the true tail-quills take an ever increasing part in forming the "nestling tail." Hence nestling feathers only function during three of the six weeks that Mallard ducklings feed and disport themselves like diving ducks. When the protoptiles are shed, the tail-quills, owing to the rhachis being short and incomplete, look unfinished. Perhaps for this reason the first set of tail-quills is ere long superseded by larger and more perfect quills in which the rhachis, as in adult ducks, ends in a fine point. Usually the first set of tail-quills begins to drop out during the fourteenth week, and a new tail consisting of feathers of the adult type is eventually developed.

The Structure of the Tail Protoptiles.—The calamus of the tail-quill, like that of the wing-quill, protoptile, continues to grow after hatching. In the case of the protoptiles at each side of the middle line the calamus only reaches a length of 4 or 5 mm. and may have only three or four "cones"; but the calamus of the outer tail protoptiles may eventually measure 15 mm. and contain over twenty "cones." I expected the entire protoptile calamus to be directly continuous with the expanded tip of the tail-quill rhachis, but I found that, as text-fig. 7 shows, the calamus splits into an outer segment continuous with the tail-quill rhachis and an inner segment continuous with the rhachis of a vestigial aftershaft, the presence of this unexpected vestige of an aftershaft indicates that even the highly specialized tail quills originally consisted of two shafts, and hence were constructed on the same plan as the double feathers of the Emu.

The shaft of the tail-quill protoptiles of a Mallard duckling as a rule consists of fourteen or more pairs of barbs, each provided with barbules. As already mentioned, the majority of the barbs of the wing-quill protoptiles are long and pointed and have only a limited number of slender barbules (Pl. II. fig. 8), but some of the barbs of the tail-quill protoptiles are ribbon-shaped (text-fig. 9), and they all have barbules along their whole length. The majority of the barbules have simple cilia along both margins; but the six or seven pairs of ribbon-shaped barbules at the tip of the protoptile have large curved cilia along one margin, which differ but little from the hooklets on the barbules forming the tip of the true tail-quills. The difference between the specialized barbules with hook-like cilia at the tip of the protoptile and the slender proximal barbules with small cilia will be evident if text-fig. 8 is compared with text-fig. 9. When the broad barbules with hook-like cilia on one edge cross each other the approximation to a true teleoptile is especially marked. What Mallard ducklings gain by having the tips of the tail-quill protoptiles highly specialized is not very obvious. The aftershaft of the Mallard's tail quill consists of eight long barbs (Plate III. fig. 11) bearing slender almost straight barbules, each with two rows of small cilia.

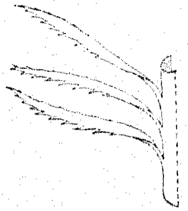
It may be mentioned that in the case of the goslings of Chinese and Emden geese the tail-quill protoptiles—though possessing a long, strong calamus firmly connected with the rhachis of the tail-quill, a well-developed shaft, and an aftershaft made up of twelve barbs—are not provided with broad distal barbules armed with hook-like cilia. In goslings, as in ducklings, the inner segment of the calamus of the tail-quill protoptile is continuous with the rhachis of a vestigial tail-quill aftershaft.

Text-figure 8.



Two of the proximal barbules of a tail-quill protoptile; they are narrow and armed with small cilia. × 64.

Text-figure 9.



Three of the broad distal tail-quill barbules armed along one edge with tooth-like cilia (*hamuli*) of true feathers. × 64. The difference between the simple proximal and the specialized distal barbules is also indicated in text-fig. 6.

(4) *The Tail-Quill Mesoptiles.*

In sixteen of the tail-quill protoptiles of the Mallard the mesoptiles are completely suppressed, but in the remaining two—the ninth from the middle line at each side—the mesoptile is represented by a simple tube from 10 to 12 mm. in length extending between the protoptile calamus and the tip of the tail-quill. This tube, though complete to start with, sooner or later splits into two or more bands, the outer of which is continuous with the rhachis of the tail-quill, while the inner ends in the rhachis of a vestigial tail-quill aftershaft. As these bands have no barbules they evidently do not represent barbs. Though there are only vestiges of two tail-quill mesoptiles in the Mallard, there are sometimes vestiges of all the mesoptiles in cross-bred domestic ducks. In cross-bred, as in Mallard ducklings, the feathers at each side of the true tail-quills approach in structure the wing-quill mesoptiles. In Eider ducklings the wing-quill, as well as the tail-quill, mesoptiles are either absent or represented by minute vestiges, hence the Eider supports the view that in the Anseres the mesoptiles no longer count in the struggle for existence.

(5) *The Prepennæ of the Trunk.*

About the prepennæ which precede the feathers of the head, neck, trunk, and hind limbs, very little need be said. In many cases the protoptiles closely resemble, and may be as large as, the wing-quill protoptiles, but they are sometimes so small and poorly developed that it is difficult to distinguish them from preplumulæ. The protoptile from the dorsal track of a thirty-eight days' Mallard duckling represented in Pl. I. fig. 1 is only half the size of the wing-quill protoptile in Pl. II. fig. 8; but some of the protoptiles of the wing-coverts are smaller than the majority of the preplumulæ. Usually the protoptiles of the trunk are shed about the same time as the wing-quill protoptiles, but in a small chequered area at each side of the body near the tail well-developed protoptiles are still present at the end of the eleventh week. Though mesoptiles precede some of the trunk pennæ, they are never as well developed as the wing-quill mesoptiles.

The examination of the mesoptiles of ducks and penguins lends support to the view that the mesoptile coat was specially acquired to meet a marked change of climate—a change perhaps from cold dry to cold damp conditions—and that in most cases as the climate improved the fur-like second coat was more or less completely suppressed, and a new coat, made up of feathers constructed on the protoptile rather than the mesoptile plan, was subsequently evolved. It is conceivable that some of our modern birds, *e.g.*, the Emu and Cassowary, are descended from ancestors which never acquired a mesoptile plumage.

2. *The Preplumulæ and Plumulæ.*

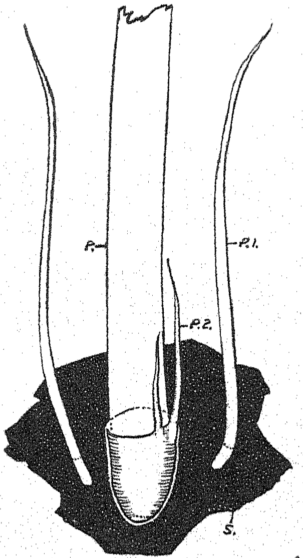
(1) *The Preplumulæ.*

In many birds the nestling coat sooner or later consists of preplumulæ as well as prepennæ. In the Gannet the preplumulæ appear before the prepennæ, and grow so rapidly that even when the prepennæ are well developed they are difficult to find; but in the Mallard in most regions the preplumulæ are hidden by a relatively dense coat of protoptiles. Though the preplumulæ papillæ in the Mallard appear three or four days later than the protoptile papillæ, the majority of the preplumulæ are ready to escape from their filaments as soon as the duckling is hatched.

The relative size of the protoptile and preplumulæ filaments of the Mallard is indicated in Pl. III. fig. 9 and in text-fig. 10. The difference in size of the protoptiles, preplumulæ, and prefiloplumæ is made evident by Pl. V. fig. 17, which shows a protoptile, three plumulæ, each with a preplumula on its tip, and, on the left of the protoptile, a prefilopluma on the tip of a developing filoplume.

The preplumula consists of a short conical calamus, a shaft often consisting of a short rhachis and four barbs, and an aftershaft also as a rule consisting of four barbs. It is sometimes difficult to distinguish the small protoptiles which precede small true feathers from preplumulæ, but when in ducklings the barbules are characterized by nodular swellings and very few cilia it may be safely assumed that the nestling feather under examination is a preplumula.

Text-figure 10.



Filaments from a Mallard embryo.
P, proximal part of a protoptile filament. *P*.1, a preplumula filament.
P.2, a prefiloplume filament. *S*., skin.

(2) *The Plumulæ.*

At the beginning of the Jurassic Age the coat of birds may have consisted only of protoptiles and preplumulæ; but in many recent birds the plumulæ form a very important part of the nestling plumage. From Pl. V. fig. 17 it may be inferred that during the fifth week the plumulæ form an inner coat as effective in preventing a loss of heat as the woolly under coat of wild sheep.

Like plumose or metaptile feathers, the plumulæ vary in size, colour, and structure, but they, as a rule, consist of a calamus, a shaft, and an aftershaft. The calamus, especially well developed in the Eider Duck, is barrel-shaped and contains relatively large cones. As it leaves the skin it divides into two portions, an outer which forms the short rhachis of the shaft, and an inner which forms the still shorter rhachis of the aftershaft (Pl. V. fig. 18). The shaft consists of a dozen or more pairs of very long slender barbs from which spring numerous slender barbules, the proximal portions of which are characterized by pyramidal swellings, while the distal portions like the preplumulæ have nodular swellings. The aftershaft (Pl. V. fig. 18) is always well developed, and like the shaft is largely made up of long barbules having the characteristic pyramidal swellings. When a plumula is shed the tip of the sheath of the growing new plumula is often found attached to the calamus. Evidence of this we have in Pl. V. fig. 19.

(3) *Prefiloplumæ and Filoplumæ.*

Nitzsch, in his account of filoplumæ, says they are strikingly distinguished from the other three kinds of feathers (contour, down, and semiplume feathers) by their peculiar position, their extraordinary slenderness, and by the entire deficiency or very small size of their vane; but he states subsequently that he believes the narrow white downy feathers of the Cormorant must be regarded as filoplumes, even though they are furnished with perfect vanes. Nitzsch further mentions that filoplumes are "associated with the contour feathers, one or even two filoplumes standing quite close to every contour feather of the head, neck, and trunk, apparently issuing almost out of the same pouch of the skin." Filoplumes are usually regarded as degenerate feathers because during development they have barbs arranged after the fashion of a down (plumula) feather.

In the Mallard during development there are usually two or more minute filaments at each side of the filaments containing the wing-quill protoptiles. These minute filaments contain prefiloplumæ. In text-fig. 10 the two short filaments (P. 2) lying in contact with the large protoptile filament are prefiloplume filaments.

In the newly-hatched duckling the minute prefiloplumæ and the large wing-quill protoptiles escape simultaneously from their sheaths—being barely visible to the naked eye, the prefiloplumæ have apparently hitherto escaped the notice of ornithologists. In course of time, as the protoptiles are pushed from the skin by mesoptiles, the prefiloplumæ are pushed from the skin by filoplumæ. The wing-quill protoptile of a thirty-eight days' duckling represented in Pl. II. fig. 8 is attached to a developing mesoptile. At the base of the mesoptile are three young filoplumes, two of which support prefiloplumes—a young filoplume with a prefiloplume attached to its tip is also seen in Pl. V. fig. 17.

Notwithstanding their small size, the prefiloplumæ have the structure of prepennæ. They are hence not dwarfed preplumulæ, as their name suggests, but dwarfed protoptiles. It is important to note that, though several developing filoplumæ may be intimately related to a protoptile, they are not imbedded in its sheath; each projects from a separate pit in the skin. At the end of the seventh week, when the filoplumes have reached a length of about 20 mm., they are still found in contact with the developing true feather. A filoplume from a forty-eight days' duckling, still carrying the minute prefiloplume on its tip, is represented in Pl. V. fig. 20. At this stage the filoplume still consists of a calamus, a shaft and an aftershaft; but as the duckling increases in size the filoplumæ in connection with the wing-quills degenerate. Each loses its prefiloplume, its aftershaft, and most of the barbs of its shaft, with the result that, as a rule, only the rhachis of the shaft and two or three vestigial terminal barbs are left.

That the filoplumes are degenerate pennæ is supported by a study of the foot-feathers of the Barn Owl (*Strix flammea*). In a newly-hatched Barn Owl one large and two small filaments are seen projecting from under the foot-scales. Soon a well developed protoptile escapes from the large mesial filament and a minute protoptile from each of the two small filaments. In course of time a simple plumose feather (metaptile), with a large aftershaft, but with a rhachis which suggests a filoplume, succeeds the large protoptile, and typical hair-like filoplumes succeed the small protoptiles.

If further proof were needed in support of the view that filoplumes are degenerate pennæ, it is obtained by the examination of the white neck feathers which form part of the nuptial plumage of Cormorants, *i. e.*, the feathers Nitzsch assumed were filoplumes. Instead of regarding the narrow neck feathers of Cormorants as filoplumes, it would be better to regard them as true feathers (metaptiles) which have undergone degeneration.

It may be added that, notwithstanding the small size of the prefiloplumæ, a microscopic examination clearly proves that they are more intimately related to protoptiles than to preplumulæ. Seeing that the filoplumes are degenerate pennæ, it might be better if the name filopenna were substituted for filopluma.

II. The Composition of Feathers.

The feathers forming the coat of the adult Emu consist of a calamus and two blades, an outer, the shaft, and an inner, generally known as the aftershaft; the wing- and tail-quills of ducks consist of a calamus and a well-developed shaft, but there is only a minute vestige of an aftershaft. Hitherto it has been taken for granted that a feather with only a vestige of an aftershaft is more primitive than a feather with an aftershaft as long and as complex as the shaft, that, in fact, the aftershaft is not a primitive but a secondarily acquired feature. The chief reasons given for regarding the aftershaft as an accessory and secondarily acquired structure are: (1) that the aftershaft is developed from a forward elongation of the calamus, and (2) that the tip of the aftershaft of the new feather is never attached to the calamus of the feather about to be shed—that, for example, in the Emu the tip of the aftershaft of the feather of the second generation is from first to last free.

If I succeed in showing that the aftershaft, like the shaft, grows from apex to base and is completed before the calamus is formed and that, during development, the tip of the aftershaft is connected with the calamus of the feather about to be shed—is, in other words, for a time attached to the old feather—it may be safely assumed that the aftershaft is a primitive feature, and that a complete true feather (penna) like a down feather (plumula) consists of two shafts or blades.

Owen evidently assumed that a true feather was made up of a calamus and a single shaft, for he states that "besides the parts which constitute the perfect feather there is an appendage attached to the upper umbilicus called the accessory plume" (**4**). According to Nitzsch, the aftershaft "originates from the underside of the umbiliciform pit" (**5**). Gadow, in discussing the aftershaft, states that when present it is developed as "a ventral elongation of the calamus," and points out that if we consider the various types of nestling feathers "with reference to the presence or absence of an aftershaft in the Teleoptiles, we are led to conclude that this appendage and consequently also the double feathers of certain Ratitæ are secondarily acquired not primitive features" (**6**).

That the aftershaft is a primary feature was suggested in 1903 by Degen in a paper on Ecdysis. In the chapter on "Adventitious Plumage," Degen writes: "I may mention here that owing to the yet more primitive conditions of the feathers of the trunk in some Ratitæ, the extreme tips of the aftershafts, which in the Cassowary and the Emu attain a length equal to that of their main shafts, *jointly support the new-growth feather* with the latter" (**7**). But Degen, following Gadow, seems to adopt the view that the calamus is concerned with the formation of the aftershaft, for he assumes that while the one half of the calamus "deposits *substantia rhachidis externa* for the main shaft, the other half deposits" the same substance required in the building up of the other shaft! Obviously the best way to throw light on the status of the aftershaft is to study its development.

1. *The Development of the Aftershaft of Plumulæ.*—In the Mallard a preplumula consists of a small conical calamus, a shaft usually made up of four barbs, two of which coalesce to form a short rhachis, and of an aftershaft also made up of four barbs. Soon after hatching the preplumulæ are pushed from the skin by plumulæ. Some of the plumulæ at the end of the fifth week, though still bearing preplumulæ on their tips, are 15 mm. in

length and consist of two distinct bundles of barbs—a large outer bundle in a line with the shaft of the preplumula and a smaller bundle in a line with the aftershaft.

In the plumula from a five weeks' duckling represented in Pl. VI. fig. 21, the outer bundle already consists of a rhachis and eight pairs of barbs, but the inner or aftershaft bundle only consists of five pairs of barbs. By the end of the sixth week the development of both the shaft and aftershaft is complete, and the unsplit portion of the epidermic tube is giving rise to a calamus. In the completed plumula (Pl. V. fig. 18) the shaft consists of a rhachis and over twenty pairs of barbs; and the aftershaft of a rhachis with about a dozen pairs of barbs.

From Pl. VI. fig. 21 it is evident that the aftershaft of a plumula in its development and structure agrees with the shaft; as it is developed before the calamus it cannot be regarded as a secondarily acquired appendage produced from a forward elongation of the calamus.

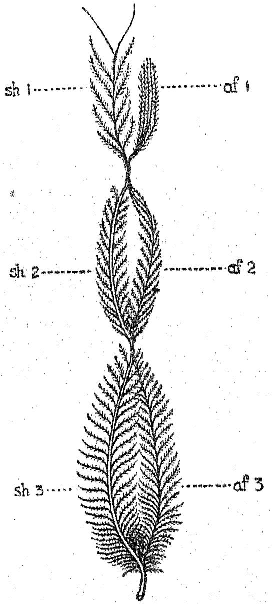
2. *The Development of the Aftershaft of Emu Feathers.*—It has hitherto been often assumed that in the Emu the protoptile has "no distinct aftershaft." That there is an aftershaft in the first, as well as in the second and third Emu feathers, is indicated by the diagram, text-fig. 11. In the young Emus I have examined the protoptile aftershaft has, with rare exceptions, consisted of seven or more barbs longer than, or at least as long as, the barbs of the shaft. In the Emu protoptile given in Pl. VI. fig. 22, the aftershaft has a short rhachis. It is especially noteworthy that in the Emu the rhachis of the protoptile shaft, instead of ending in a hollow calamus containing "cones," is connected with the relatively thick rhachis of the shaft of the feather of the second generation by a solid band (Pl. VI. fig. 23).

In a like manner the rhachis of the protoptile aftershaft is connected with the aftershaft rhachis of the second feather. When, as sometimes happens, the connecting bands occupying the position of a calamus separate from each other (Pl. VI. fig. 23), it becomes obvious that the tip of the aftershaft of the second feather is not free as generally assumed, but from the outset continuous with the protoptile aftershaft.

Though as in plumulæ the rhachis of the aftershaft is formed by the fusion of two barbs, the distal portion of the rhachis of the shaft is simply a continuation of the band proceeding backwards from the protoptile shaft. That the aftershaft of the feathers of the second generation is not "developed as a ventral elongation of the calamus," but develops from apex to base like the shaft, is made clear by Pls. VI. and VII. figs. 23, 24, & 25, which show the second feather at various stages of growth.

As the destined length of the second-generation feather is reached the rhachis of the shaft expands, gives off six or more pairs of relatively long barbs, and thereafter becomes continuous with the rhachis of the shaft of the feather of the third generation (Pl. VII. fig. 26). In a like manner the proximal end of the rhachis of the aftershaft, after giving off several pairs of barbs but without appreciably increasing in width, becomes continuous with the rhachis of the aftershaft of the feather of the third generation (Pl. VII. fig. 26). When (as was the case in the specimen represented in Pl. VII. fig. 27) the two connecting bands naturally separate from each other, it is impossible to escape

Text-figure 11.



In this diagram the structure and relations of the feathers forming the first three generations in the Emu are indicated. *sh.* 1, shaft, and *af.* 1, aftershaft of protoptile. *sh.* 2, shaft, and *af.* 2, aftershaft of a feather of the second generation. *sh.* 3, shaft, and *af.* 3, aftershaft of a feather of the third generation. The aftershaft of the protoptile is from the outset free, but the tip of the aftershaft of the feather of the second generation is, to start with, continuous with the protoptile aftershaft, and the aftershaft of the feather of the third generation is also for a time continuous with the aftershaft of the second generation feather—according to Gadow the tip of the aftershaft of the second generation feather is a forward prolongation from the calamus which is never during development connected by its tip with the "calamus" of the protoptile or first generation feather.

from the conclusion that, just as the aftershaft of the second feather of the Emu is connected at the outset with the protoptile, the aftershaft of the feather of the third generation is connected with the feather of the second generation.

The feathers represented in Pl. VII. figs. 26 & 27 (from a seven months' Emu bred in the Gardens of the Zoological Society of London) prove conclusively that in the Emu the aftershaft in origin and structure agrees with the shaft, while the feathers represented in Pl. VII. figs. 24 & 25 (from a much younger Emu in the Museum of the Philosophical and Literary Institute, Leeds) as clearly indicate that as the aftershaft is developed before the calamus it cannot be an outgrowth from the calamus. The first three generations of the feathers of an Emu are diagrammatically represented in text-fig. 11.

Before dealing with the aftershaft in the Carinatæ, attention may be directed to the remarkable Emu feather of the second generation represented in Pl. VIII. fig. 28. In this growing feather the aftershaft, instead of resembling the shaft, simply consists of two barbs bearing barbules. An Emu feather with an aftershaft represented by two simple barbs is interesting, because in true feathers near the oil-gland of ducks two long barbs sometimes occupy the position of an aftershaft. That the two long barbs in this Emu feather represent a phase in the degeneration of the aftershaft is suggested by Pl. VIII. fig. 29, a developing true feather with the protoptile intact from the rump of an eighteen days' Mallard duckling. Connected with the protoptile calamus are two bundles of barbs—a large bundle with a distinct rhachis which is obviously a developing shaft and a smaller bundle representing an aftershaft. The smaller or aftershaft bundle is connected to the inner aspect of the protoptile calamus, as in the Emu feather, by two long barbs. In course of time the large bundle in Pl. VIII. fig. 29 would have developed into a shaft like the one represented in Pl. I. fig. 1, and the small bundle into an aftershaft with a short rhachis. Possibly long barbs which represent an aftershaft will be met with in the feathers of other Ratitæ.

The two long barbs in the Emu feather in Pl. VIII. fig. 28 support the view that the coat of the adult Emu consists of true feathers and not, as Pycraft suggested, of mesoptiles.

3. *The Development of the Aftershaft of the True Feathers of Penguins.*—In the Ringed Penguin the protoptiles though umbelliform may be said to consist of two sets of barbs—an outer representing a shaft and an inner occupying the position of an aftershaft. Though in ducks and geese there is a well-developed protoptile calamus containing "cones," in penguins as in the Emu a true protoptile calamus is never developed. Soon after the protoptile escapes from its sheath the part of the epidermic tube representing a calamus splits into slender cords, which connect the barbs of the protoptile with barbs of the developing mesoptile. The mesoptile consists of a shaft made up of seven or more simple barbs which end in the tip of the true feather, and of a complex aftershaft connected with the aftershaft of the true feather. In text-figs. 3 & 4 the mesoptile aftershaft is connected to the aftershaft of the true feather by a narrow band formed by the fusion of the distal portions of the barbs of the

aftershaft of the true feather. Pycraft considered the "ribbon-shaped stem" connecting the mesoptile to the aftershaft of the true feathers as somewhat remarkable, because "in all other instances yet known the nestling-down when attached to contour feathers is attached to the rami (barbs) of the main shaft" (9). When it is realised that in Penguins the mesoptile may have a well-developed aftershaft the connection of the mesoptile with the aftershaft of the true feathers ceases te be remarkable. Though in the Ringed Penguin the mesoptile aftershaft is decidedly larger and more complex than the shaft, it is developed at the same time as the shaft, and is directly continuous with the aftershaft of the true feathers. That in Penguins the aftershaft of the true feathers has the same origin as the shaft is made abundantly evident when the development of the feathers of the fourth generation is studied. In Pl. VIII. figs. 30 & 31 we have feathers from a moulting King Penguin in the Scottish Zoological Park. From fig. 30 it is evident the new feather has from the first been double, consisted of outer barbs representing a shaft and of inner barbs in the position of an aftershaft. Had the development proceeded the tip of the aftershaft would have been set free when the old feather was shed. In fig. 31, the shaft having been removed, the aftershaft is seen emerging from the tip of the sheath which invested the growing feather. These figures show that in Penguins the aftershaft of a feather of the fourth generation is for a time as complete as in the Emu. The aftershaft of the mesoptile and of the first true feather of a Ringed Penguin are diagrammatically represented in text-figs. 3 & 4.

4. *The Development of the Aftershaft in the Ptarmigan, the Common Fowl, and the Guillemot.*—As already mentioned, it has been suggested that in Grouse, Fowls, and other Galli the feathers forming the first nestling coat may correspond to the mesoptiles forming the second nestling coat of Penguins. Against this view it may be pointed out (1) that unlike the mesoptiles, but like the protoptiles of Penguins and Ducks, the first nestling feathers of the Galli are developed in filaments; (2) that in structure they are intermediate between the protoptiles of Penguins and Ducks; and (3) that they are sometimes succeeded by vestiges of mesoptiles. Degen mentions that in Grouse the aftershaft may be two-thirds the length of the shaft but, as Pl. IX. fig. 32 shows, the aftershaft in Grouse may be as long and as complex as the shaft—the only difference in the feather figured apart from its width is that, as in the Emu, the rhachis of the aftershaft is slightly shorter than the rhachis of the shaft. In the Ptarmigan the protoptile often consists of fifteen barbs, eight representing a shaft with a short rhachis, and seven forming an aftershaft also with a short rhachis. From the protoptile calamus there proceed about twenty barbs, which in some cases readily separate into three distinct bundles—a large one destined to form the tip of the shaft, and two small ones which later unite to form the tip of the

aftershaft. In some metaptiles the rhachis of the shaft extends to the tip of the feather, in others it ends in two slender barbs some distance from the tip. Though at the outset in Grouse both the shaft and the aftershaft of the true feather may consist of several more or less distinct bundles, sooner or later the outer barbs give rise to the shaft, while the inner form an aftershaft. When the destined number of barbs for the shaft and aftershaft have been produced the splitting of the epidermic tube is arrested, and steps are taken to form a calamus in which "cones" make their appearance. Evidently in Grouse, as in Penguins, the aftershaft is not a forward elongation of the calamus. An interesting stage in the development of a Ptarmigan true feather is given in Pl. IX. fig. 33.

It has been asserted once and again that "in the great feathers which form the 'quill' or 'flight' feathers (remiges) of the wing and the tail-quills (rectrices) the aftershaft is invariably wanting"*. Assuming that in the case of the wing-quills the aftershaft is invariably absent, it might be argued, that these all-important feathers differed in their origin and history from the other true feathers, that while the trunk feathers may possibly have developed from an epidermic tube, the wing- and tail-quills were formed by the splitting of elongated scales. Attention has already been directed to the fact that in the Mallard during the earlier stages in the development of the wing- and tail-quills, there is a vestige of the distal portion of an aftershaft (text-figs. 5 & 7). That in wing- and tail-quills there may also be a vestige of the proximal portion of an aftershaft is made evident by Pl. IX. fig. 34, which represents the aftershaft of a wing-quill from a full-grown Grouse.

Fowls are not supposed to have the aftershaft as well developed as Grouse, nevertheless, as Pl. IX. fig. 35 shows, the aftershaft in the silky breed may be as long as the shaft. In its development the aftershaft in the silky breed follows the same course as in Ptarmigan.

In the Guillemot the aftershaft is, to start with, sometimes as long as the shaft. A Guillemot feather from the side of the trunk is represented in Pl. X. figs. 36 and 37. In this case the protoptile consists of seventeen barbs. Of the seventeen barbs nine end in the tip of the shaft of the true feather, four end in barbs of the shaft which join the rhachis a considerable distance from the tip, and four, which represent the protoptile aftershaft, are connected with the aftershaft of the true feather (Pl. X. fig. 37).

Evidently the history of the aftershaft in Grouse, Fowls, and Guillemots affords no support to the view that the aftershaft is a secondarily acquired appendage, and may be said to fully establish the view that a complete true feather like a plumula consists of a calamus and two shafts.

---

* Pycraft, 'A History of Birds,' p. 9.

III. ORIGIN AND HISTORY OF FEATHERS.

It seems to be generally assumed by naturalists and others interested in birds that feathers are modified scales, and were originally acquired to enable birds to fly. When evidence of the scale origin of feathers is asked for, the reply usually is, "If you accept the view that birds were evolved from Reptile-like ancestors you may safely also accept the view that feathers are specialized scales." Having adopted the view that feathers are modified scales, investigators interested in the coat of birds proceeded to inquire if each feather corresponds to an entire scale or to part of a scale. Wiedersheim favoured the view that each feather represents a complete scale, but Bornstein (**13**) and others came to the conclusion that a feather papilla only represents a fragment of a scale.

How scales were transformed into feathers has been indicated by various writers. Baron Frances Nopcsa, in a paper "On the Origin of Flight," states that we may quite well suppose "birds originated from bipedal long-tailed cursorial reptiles which during running oared along in the air by flapping their free anterior extremities," and added that the double running and flapping action would subsequently easily lead to an enlargement of the posterior marginal scales of the antebrachium, and eventually to their development into actual feathers (**10**). Lull, another believer in the transmission of acquired somatic characters, points out that the anterior extremities of birds when in the making would be more effective if their breadth was increased, and that an increase of the size of the scales along the arm margin would be a ready means to this end. Lull then proceeds to say the "scales would extend, lighten, and ultimately evolve into feathers which would not only subserve the function of flight, but acting as clothing retain and aid in the increase of temperature" (**11**). Similar views are held by W. K. Gregory, who tells us the Pro-Aves jumped lightly from branch to branch and finally from tree to tree partly sustained by the long scale-like feathers of the pectoral and pelvic wings.

The view that feathers are modified scales has long been held by Pycraft. In a work published in 1910 Pycraft points out that, to start with, the body clothing of birds probably consisted of relatively large scales, "those covering the hinder border of the incipient wing growing longer would still retain their original overlapping arrangement and along its hinder border would in their arrangement, appearance, and function simulate the quills of modern birds; as their length increased they became also fimbriated and more and more efficient in the work of carrying the body through space."

It is now evident that the wing-quills of birds are preceded by nestling feathers, and may be regarded as modified protoptiles: hence the question at issue is, Are the protoptiles modified scales?

It is inconceivable that the small protoptile forerunners of the wing-quills of Ducks were evolved from enlarged scales, which as they increased in length became fimbriated. The more the history of feathers is studied the more untenable becomes the belief in their origin from scales. When special attention is directed to the phases through which feathers pass during their development, it becomes evident that in an attempt to trace their origin we are not concerned with the wing-quills or other contour feathers, but with the feather papillæ, and still more with the filaments, in which the nestling feathers are developed. It is conceivable that by the appearance of new and dominant factors in the germ-plasm, scale papillæ, instead of developing into scales, developed into feather filaments, but it is difficult to imagine how scales by growing longer and splitting were transformed into double-shafted nestling feathers. There is little chance of the geological record ever throwing any light on the origin of either feather papillæ or feather filaments, hence we must make the most of the embryological record. Thus far the embryological record has afforded no support to the view that scales in whole or in part were concerned in the making of feathers.

When birds first acquired feather filaments it is impossible to say, but we may assume that when the remote ancestors of birds and mammals became warm-blooded any outgrowths from the skin which prevented a loss of heat would from the first count in the struggle for existence.

A hint as to the nature of the coat in the progenitors of mammals we have from Armadillos, and an indication of the kind of coat worn by the Pro-Aves is obtained by studying the development of nestling feathers, more especially of the protoptiles of feather-footed birds. The Six-banded Armadillo has an extensive scaly covering, but only a sparse coat of hair; birds, with few exceptions, have during development a more or less complete coat of filaments*, and probably in Owls the foot-feathers still bear the same relation to scales as in the primeval birds. In the developing Armadillo a stage is eventually reached when hairs are seen projecting from under the developing scales or from the skin between the scales. The number of hairs developed in connection with scales varies. There are often groups of three hairs projecting from under the tail scales of mammals; in the Six-banded Armadillo there are often three or four hairs to a scale, but sometimes only one; in the small Argentine Armadillo *Chlamydophorus*, as text-fig. 12 shows, fifteen hairs may be developed in connection with one foot-scale.

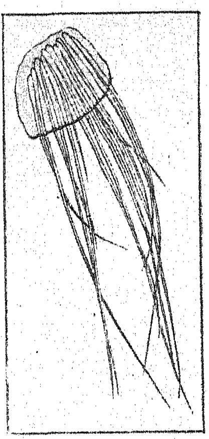
In Armadillos and other mammals having scales as well as hairs there is no evidence that the hairs are ever developed from scales.

---

* All the birds I have examined, with the exception of the House Sparrow, had a more or less complete coat of protoptiles—in the Rook a nestling coat is said to be absent, but even in Rooks there are a few well-developed nestling feathers.

That in ancient birds feathers were intimately associated with scales is suggested by the feather papillæ having approximately the same arrangement as the scales of reptiles, by feathers emerging from under scales above the tarsal joints of the Woodcock, and by chicks and ducklings having vestiges of scales in connection with the feather filaments of the legs. In the case of Grouse and other birds with only one feather emerging from under a foot-scale, we are tempted to assume that each foot-feather is developed from part of the scale it is associated with. But when we find three feathers projecting from under the foot-scales of the Barn Owl (*Strix flammea*) and seven or more feather filaments occupying an area equivalent to a foot-scale, we are less inclined to admit that each of the foot feathers of Grouse corresponds to part of a scale. When the development of the foot feathers of the Barn Owl is studied, one large and two small filaments are found projecting from many of the scales; the large filament contains a protoptile, and each small filament contains a prefilopluma. Similar groups of filaments which occur above the tarsal joint are overlapped by scale vestiges, but in the three feather groups on the head scales are conspicuous by their absence. The well-developed scales in connection with the foot-feathers and the vestiges of scales in connection with feathers above the tarsal joints support the view that birds, to start with, had a complete scaly covering and a sparse coat of feather filaments.

Text-figure 12.



Scale from the foot of the small Argentine Armadillo (*Chlamydophorus*) from under which proceed a number of hairs developed from the skin underlying the scale. The three filaments proceeding from under the foot-scales of Barn Owl embryos like the hairs associated with the scales of mammals are developed from the skin under the scales and not by a splitting of the scales or from fragments of the scales.

As in feather-footed birds the feather papillæ are from the first as distinct from the scale papillæ as the hair rudiments are distinct from scales, there seems no escape from the conclusion that the foot feathers are not modified scales. Further, when it is realized that the foot feathers often belong to a simple primitive type, have the aftershaft as long as the shaft, and that in many birds there are seven or more feathers occupying the position of an ancestral scale, we are justified in assuming that feathers, like hairs, were originally intimately related to, but not derived from, scales.

As a matter of fact, believers in the scale origin of feathers admit that the foot feathers of recent birds are not derived from the scales from under which they project. Just as it has been assumed that the aftershaft in Emu feathers is a secondarily-acquired structure, it is assumed the scales on the feet of birds are secondary structures. That the scales overlapping the feathers of modern birds were secondarily acquired and that the foot-feathers were formed from the original foot-scales, are gratuitous assumptions wholly unsupported by facts.

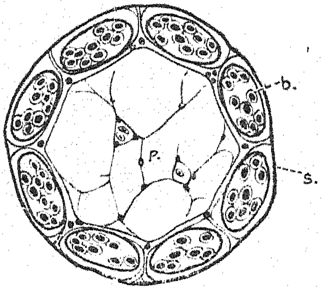
How or when feather filaments made their appearance it is impossible to say, but we may safely assume that many centuries elapsed before there was evolved in each filament a more or less complex feather; needless to say that unless a filament in which a feather was evolving was of more use than a simple filament, natural selection took no part in providing birds with their original coat of what are now familiarly known as nestling feathers. On the other hand, when one bears in mind that blood-vessels extend right to the tip of a feather filament, and not merely a short distance into its root as in a hair, it is probable that early specialization of the filaments was well-nigh inevitable. Given a constant flow of blood through the axis (pulp) of the filament, an inner epidermic layer capable of rapidly adding new cells to the middle layer, an outer epidermic layer forming a protecting sheath and, in addition, an ever increasing demand for a coat capable of arresting the flow of heat from the skin, changes were almost bound to take place in the bristle-like outgrowths projecting from under or between the scales of the remote ancestors of birds.

Judging by what takes place to-day during the development of the simple protoptiles of pigeons, the first step in the making of a feather probably consisted in the splitting of the middle epidermic layer to form hair-like barbs. The result of this splitting of the hollow cone formed from the middle epidermic layer of a pigeon filament is represented in text-fig. 13. The appearance of a completed pigeon protoptile after escaping from its protecting sheath is represented in Pl. X. fig. 38.

The protoptiles of Penguins represent a second stage in the evolution of true feathers (text-fig. 3). Like the pigeon protoptiles all the barbs are alike (form a tassel or umbel), but by sprouting they have acquired barbules.

A series of links connect the relatively simple umbelliform protoptiles of Penguins with the highly-specialized protoptiles of Ducks and Emus. There are good reasons for believing that the warm-blooded progenitors of birds and mammals were evolved out of reptile-like ancestors during a period when desert conditions prevailed. How long this period lasted, and to what extent feathers had been specialized when it came to an end it is impossible to say, but judging by what happens during the development of the wing-quills of the Mallard, it may be assumed the period of aridity came to an end, and a glacial period had fairly set in long before wing-quills and other true feathers were evolved. In other words, before protoptiles had been modified to form metaptiles and teleoptiles, progress in the evolution of true feathers was arrested owing to the necessity of providing birds with a fur-like coat as capable of arresting the flow of heat from the skin as the dense coat now worn by Polar Bears and other Arctic mammals.

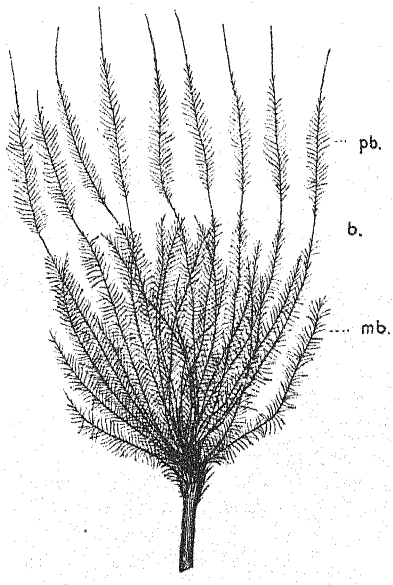
Text-figure 13.



Section through the filament of a Pigeon in which the middle epidermic layer has been split longitudinally to form barbs. *s.*, the thin sheath which disintegrates immediately after hatching. *b.*, one of the eight barbs formed by the splitting of the hollow cone formed by the middle epidermic layer. *p.*, the pulp containing blood vessels, *i. e.*, the dermis or true skin which extends during development to the tip of the protoptile. After Davies.

The discovery by Dr. Eagle Clarke and Mr. Pycraft of a mesoptile coat in penguins has profoundly modified our views about the plumage of birds. We do not yet know if the remote ancestors of all our modern birds acquired a mesoptile coat—probably in the case of the ancestors of the Ratitæ this was unnecessary—but the more the nestling feathers are studied the evidence of the existence of two coats of prepennæ in the ancestors of modern birds is increased. The fur-like mesoptile coat is probably as well developed to-day in penguins as it was in their remote ancestors of the Jurassic Age; relatively large mesoptiles still occur in ducks and geese, and I have found recently distinct vestiges of a mesoptile coat in pigeons. How long birds, or most of them, in order to survive required a fur-like coat throughout life we have no means of knowing; but this much is certain, that in most recent species of birds the mesoptile coat is in the act of being suppressed, or has already disappeared—even in the King Penguin chicks it is probably never worn in the Antarctic for more than 9 or 10 months. From what we know about the mesoptile coat it seems to have been originally produced partly by lengthening the protoptiles and partly by the development of new barbs. This is suggested by text-fig. 14, which represents a developing mesoptile feather from the breast of an Adélie Penguin. The nine barbs forming the protoptile are directly continuous with nine mesoptile barbs; the rest of the mesoptile consists of barbs having no connection with the protoptile. As Pycraft points out, the second coat of the Adélie Penguin is "a

Text-figure 14.



A developing mesoptile of an Adélie Penguin. In penguins the mesoptiles consist, as a rule, of numerous barbs which in some areas may reach a length of over three inches. A true protoptile calamus containing "cones" though present in ducks is seldom met with in other birds. As the protoptile is pushed from the skin the inner ends of the protoptile barbs, destitute of barbules, separate from each other and are subsequently seen to be continuous with mesoptile barbs. *mb.*, one of the numerous barbs of the developing mesoptile. *pb.*, one of the nine protoptile barbs, each of which is connected with a mesoptile barb. *b.*, one of the nine slender cords which together for a time played the part of a protoptile calamus.

long, dense woolly covering, so dense that it is difficult to expose the skin." In course of time the protoptile coat is shed and the mesoptile coat is pushed from the skin by the true feathers.

The long fur-like mesoptile coat of the King Penguin suggests that during the Ice Age, which succeeded the period of desiccation, the evolution of true feathers was arrested, and that the mesoptiles cannot be regarded as representing a stage in the evolution of true feathers. Though to the naked eye the mesoptile barbules seem to be identical with the barbules forming the protoptiles, they are seen to differ when examined under the microscope—instead of being nearly straight they are spirally twisted at their origin. In the case of King Penguin chicks the mesoptiles differ from the protoptiles more than in the Adélie chicks, and, as already pointed out, the mesoptiles of the Ringed Penguin decidedly differ from both the protoptiles and the metaptiles. In all the three Penguins mentioned the first true feathers differ from the prepennæ which precede them. Hence, though the prepennæ and all the true feathers which succeed them must be regarded as links in a chain, it should be borne in mind that the first link differs both in function and structure from the second, and the second from the third. Further, it should be borne in mind that there are good reasons for believing that, but for the advent of an Ice Age, the protoptiles at a comparatively early period would have been succeeded by true feathers, and that probably long before Archæopteryx made its appearance on the scene some millions of years ago, steps would have been taken in most birds to suppress the fur-like coat of mesoptiles, now apparently only well developed in Penguins.

In conclusion, it may be stated that a study of the development of birds suggests: (1) that their coat, to start with, consisted of various kinds of simple filaments; (2) that in course of time the hollow epidermic cone in each filament, in some incomprehensible way, was converted into a protoptile or preplumula: (3) that the protoptiles in some cases soon acquired the chief characteristics of true feathers; (4) that for a time progress was arrested in order to provide birds (or most of them) with a fur-like (mesoptile) coat, by way of giving them a chance of surviving during the cold phases of an Ice Age: (5) that as the climate improved the mesoptile coat was in many cases superseded by a coat of true feathers; and (6) that by the specialization of feathers along the posterior margin of the hands and forearms and the sides of the tail, birds of the Archæopteryx type were eventually evolved capable of flight, or at least of gliding easily from tree to tree.

Text-figures 1, 2, 8, 9, 12 are from drawings by Miss Augusta Lamont, B.Sc., text-figures 3–7 and 10, 11, 13, 14 are from drawings by the author, all the other figures are from photographs by Mr. John Chisholm.

Towards defraying the cost of the drawings and photographs a grant was obtained from the Moray Fund of the University of

Edinburgh and a grant has been voted from the Carnegie Trust for the Universities of Scotland, towards the cost of publishing this paper.

In addition to material in the form of ducklings, goslings &c., bred at Craigybield, Penicuik, it ought to be mentioned that valuable contributions for the study of nestling feathers were provided by the Director of the Zoological Society of Scotland, and that but for the Institution of the Scottish Zoological Park I would not have been led to undertake research work on the Structure and History of Feathers. Further, it ought to be mentioned that during the investigation I received valuable material from the Zoological Society of London, the Royal Scottish Museum, and the Philosophical and Literary Institute of Leeds, and that I am especially indebted for specimens that proved most useful to Colonel Ashley, M.P., Miss Clerk of Penicuik, William J. Gordon, Esq., of Windhouse, Yell, Shetland, Professor Meakins, the University of Edinburgh, and Professor Philip J. White, the University of North Wales.

References to Literature cited in Paper.

1. Ingram, Collingwood.—‘The Ibis,’ October 1920, p. 856.
2. Gadow, Hans F.—Newton's ‘Dictionary of Birds,’ p. 243.
3. Pycraft, W. P.—“The Emperor and Adélie Penguins,” Nat. Ant. Expedition, Zoology, vol. ii. p. 12. 1907.
4. Owen, R.—Comparative Anat. vol. ii. p. 235.
5. Nitzsch.—‘Pterylography,’ English Translation, p. 8. 1867.
6. Gadow, Hans F.—Newton's ‘Dictionary of Birds,’ p. 245.
7. Degen.—Trans. Zool. Soc. vol. xvi. pp. 362 & 363.
8. Pycraft, W. P.—Trans. Zool. Soc. vol. xv. p. 164.
9. ,, ,, Nat. Ant. Expedition, Zool. vol. ii. pp. 7 & 8.
10. Nopcsa.—Proc. Zool. Soc. 1907.
11. Lull.—‘Organic Evolution,’ pp. 533 & 534. 1917.
12. Pycraft.—‘A History of Birds,’ p. 39. 1910.
13. Bornstein.—Archiv f. Naturgesch., Band I. Supplement, heft 4.

EXPLANATION OF THE PLATES.

Plate I.

Fig. 1. Protoptile and metaptile from vicinity of preen gland of a 38 days' Mallard. The mesoptile has been suppressed. The long barbs proceeding from the inner aspect of the protoptile calamus towards the calamus of the metaptile are vestiges of a metaptile aftershaft. × 2.

2. Protoptile, mesoptile, and tip of a wing-quill of a 5 weeks' Indian Runner duckling.

3. Protoptile, mesoptile, and tip of a wing-covert of a 6 weeks' Emden gosling.

4. Tip of tail-quill of a young Ringed Penguin (n. s.).

Plate II.

Fig. 5. Tail-quill and protoptile of a 5 weeks' Mallard duckling (n. s.).

6. A 10 days' Mallard embryo. The tail-quill papillæ are well developed, but there is little indication of the wing-quill papillæ.

7. Wing of a 25 days' Mallard duckling showing the wing-quill protoptiles (n. s.).

8. Wing-quill protoptile from a five weeks' Mallard duckling attached to tip of developing mesoptile.

PLATE III.

Fig. 9. Filaments from a 13 days' Mallard embryo; the long filaments contain developing protoptiles, the small ones preplumulæ or prefiloplumæ. × 2.

10. Wing-quill protoptile artificially removed from a filament of a 26 days' Mallard embryo.

11. Aftershaft of the protoptile of a duckling.

12. Wing of a 38 days' Mallard duckling showing mesoptiles between the protoptiles and the developing primary and secondary wing-quills. Lying between developing wing-quills (each still invested by a sheath) are wing-coverts in which the mesoptile is vestigial.

PLATE IV.

Fig. 13. Protoptile, mesoptile, and tip of wing-quill of a Chinese gosling. Though the mesoptile seems to be umbelliform and to end in a calamus, it really consists of a shaft and an aftershaft from which slender threads proceed to the tip of the true feather.

14. In this figure the proximal portion of the mesoptile is represented. It consists of a narrow, perforated band representing the rhachis of the mesoptile shaft, of a broad perforated band representing the rhachis of the aftershaft, and of numerous slender threads which connect these bands with the shaft and the vestigial aftershaft of the true feather.

15. Nestling tail of a 7 days' Mallard duckling. The protoptiles at each side of the middle line have been pushed from the skin by the developing true tail-quills.

16. The "nestling tail" at the middle of the fifth week. It now consists of growing true tail-quills as well as of protoptiles, usually with the exception of the ninth from the middle line at each side the protoptiles are directly continuous with the tail-quills—in other words, in the tail of the Mallard duckling nearly all the mesoptiles have been completely suppressed.

PLATE V.

Fig. 17. Nestling feathers from the back of a 33 days' Mallard duckling. The large protoptile has a distinct calamus containing "cones." To the left of the calamus are: (1) a filoplume with a minute prefiloplume on its tip; and (2) two plumulæ each carrying a preplumula, to the right a plumula with *a preplumula on its tip*. × 5.

18. A plumula from a young Aylesbury duck showing a large shaft consisting of long, slender barbs springing from a relatively short rhachis and a well-developed aftershaft with a short rhachis.

19. The calamus of a naturally shed plumula with part of the sheath of the growing plumula attached.

20. A developing filoplume with a prefiloplume at its tip from a 7 weeks' Aylesbury duckling. × 2·5.

PLATE VI.

Fig. 21. Developing plumula from a 5 weeks' duckling. The aftershaft is developing from apex to base in exactly the same way as the shaft. × 4.

22. A protoptile from a young Emu showing an aftershaft with a short rhachis.

23. Emu feathers of the first (protoptile) and second generation. The protoptile shaft is directly continuous with the shaft of the second feather, and the protoptile aftershaft is continuous with the aftershaft of the second feather.

PLATE VII.

Figs. 24 & 25. In 24 we have an early stage in the development of an Emu feather of the second generation. In 25 the development of the second generation feather has been nearly completed. In both cases the aftershaft is developed in the same way as the shaft—the tip of the aftershaft of the second feather is continuous with the protoptile aftershaft and the tip of the shaft is continuous with the protoptile shaft.

Fig. 26. Emu feathers of the first, second, and third generations. The tip of the aftershaft of the feather of the third generation is continuous with the rhachis of the aftershaft of the feather of the second generation.

27. In this specimen the tip of the aftershaft of the second generation feather had lost its connection with the protoptile, and the tip of the aftershaft of the third generation feather had lost its connection with the "calamus" of the feather of the second generation.

Plate VIII.

Fig. 28. Emu protoptile and a developing feather of the second generation, the aftershaft of which is represented by two barbs. × 5.

29. Developing feather from rump of 18 days' Mallard duckling. This feather consists of two portions, one, the larger, representing a shaft, and one representing an aftershaft, connected like the Emu feather given in fig. 28, to the protoptile by two barbs.

30. Breast feathers from an adult moulting King Penguin. The growing feather consists of a shaft and an aftershaft connected by their tips with the calamus of the feather about to be shed.

31. In this figure the shaft of the new feather has been removed to show the connection between the developing aftershaft and the old feather.

Plate IX.

Fig. 32. Grouse feather with an aftershaft as long and as complex as the shaft.

33. A protoptile and a developing true feather from a young Ptarmigan. The part of the developing feather with a distinct rhachis represents the shaft, the part in which a rhachis has not yet appeared represents an aftershaft.

34. Calamus and aftershaft of the wing-quill of a Grouse.

35. Feather of a fowl of the Silky breed with an aftershaft as long as the shaft.

Plate X.

Figs. 36 & 37. Feather from a nestling Black Guillemot. 36, represents the shaft, and thirteen barbs of the protoptile. 37, the four remaining protoptile barbs connected with the rhachis of the aftershaft which was detached along with the calamus.

38. Protoptile of a Wood Pigeon connected to the tip of a true feather by a vestige of a mesoptile. The pulp projects from the tip of the teleoptile. Note that the barbs resemble hairs, have no barbules.

EXHIBITIONS AND NOTICES.

May 10th, 1921.

Dr. A. Smith Woodward, LL.D., F.R.S., Vice-President, in the Chair.

Sir S. F. Harmer, K.B.E., F.R.S., exhibited a mounted specimen of a young female *Rhinoceros sondaicus*, the one-horned "Javan Rhinoceros," presented by T. R. Hubback, who shot it in Lower Tenasserim, to the British Museum (Natural History). Attention was called to the absence of a horn in the female, a character which Mr. Hubback believes to be normal. A young male of this species, from Java, was formerly exhibited in the Society's Gardens, and was described by Dr. P. L. Sclater, F.R.S. (P. Z. S. 1874, p. 182; Trans. Z. S. ix. p. 649). Although osteological material is to be found in various Museums, there appear to be extremely few mounted specimens in existence. The Javan Rhinoceros, which formerly ranged from Assam to Lower Bengal, the Malay Peninsula, and Java, has become increasingly rare during recent years, and it is in urgent need of protection. Its occurrence in Sumatra and Borneo has been questioned, but reference was made to the statements of W. Volz ('Nord-Sumatra,' vol. ii. p. 372, Berlin, 1912), as proving its occurrence, in limited numbers, in North Sumatra.

Mr. Thos. Gerrard, F.Z.S., exhibited, and made remarks upon, a series of photographs of the skeleton of an old male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie), the property of Lord Rothschild, and also a series of photographs showing the milk-dentition in the skull of a young African Elephant.

On behalf of Lord Rothschild, Mr. Gerrard exhibited a specimen of a male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie) mounted by Messrs. Rowland Ward, and stated that it differed from the other races of Gorilla externally by its long, thick pelage, intense black colouring, and the large fleshy protuberance on the top of the head, which often measured 6 inches by 6 inches (*i. e.* width and height). The skull was much wider at the occiput even than in *G. gorilla matschiei* Rothschild. The specimen was a very aged male, long past the age of reproduction, and was found solitary, several miles from the two herds inhabiting the region. The specimen was of great pathological interest, as it was the first instance known of pyorrhœa alveolaris in a Gorilla. Habitat Mikeno Volcano, Kivu District.

Mr. D. Seth-Smith, F.Z.S., exhibited a series of skins and photographs of some polyandrous Birds, and described their mating habits.

Dr. Chas. F. Sonntag, F.Z.S., exhibited and made remarks upon, some abnormalities in the Carnivora.

Mr. L. T. Hogben, F.Z.S., and Mr. E. A. Spaul exhibited, and made remarks upon, the effect of Pineal Gland administration on the pigment-cells of Frog Tadpoles.

May 24th, 1921.

Prof. E. W. MacBride, D.Sc., F.R.S., Vice-President,
in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of April:—

The registered additions to the Society's Menagerie during the month of April were 198 in number. Of these 81 were acquired by presentation, 27 were deposited, 84 were purchased, and 6 were born in the Menagerie.

The following may be specially mentioned:—

A pair of Lion Cubs (*Felis leo*), from Somaliland, presented by Sir Geoffrey Archer, K.C.M.G., on April 21st.

2 Sloth-Bear Cubs (*Melursus ursinus*), from the Central Provinces of India, presented by Capt. R. C. Ansdell on April 5th.

2 King Vultures (*Gypagus papa*), from Tropical America, purchased on April 6th.

2 Spot-billed Toucanets (*Selenidera maculirostris*), from Brazil, purchased on April 28th.

A collection of Tropical Fish, including several species new to the Collection, purchased on April 6th.

Miss L. E. Cheesman, F.E.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the habits, in the larval stage, of the Hydropsychidæ (Snare-building Caddis Worms).

Major STANLEY S. FLOWER, O.B.E., F.Z.S., exhibited examples of three species of Egyptian Jerboas—*Jaculus jaculus*, *Jaculus orientalis*, and *Scarturus tetradactylus*, the latter being the first living specimens ever brought to England; and made remarks upon the distribution of the three species in North Africa.

June 7th, 1921.

Prof. J. P. HILL, F.R.S., Vice-President,
in the Chair.

Major STANLEY S. FLOWER, O.B.E., F.Z.S., exhibited, and made remarks upon, some living specimens of *Testudo leithii* and ar example of *Testudo ibera*.

Dr. P. CHALMERS MITCHELL, C.B.E., F.R.S., exhibited, and made remarks upon, a photograph of the Death-mask of a young Gorilla, presented to the Society by Prof. Howard Macgregor, of Columbia University, New York.

Dr. FRANK M. CHAPMAN gave an account of the distribution of Bird-life in the Urubamba Valley of Peru, and of his expedition down the Urubamba river from its sources in the Puna zone, at an elevation of 14,200 feet, to the Tropical zone at 3500 feet. He reviewed the existing climatic conditions in Peru, and commented on the faunal characteristics of the Puna, Temperate, Subtropical, and Tropical zones encountered in the descent. A comparison of the Avifauna of the forests of the humid Temperate zone (alt. 10,000–12,500 ft.) with that of the adjoining treeless, grass-grown plains and slopes of the Puna zone, showed that that of the first-named area has evidently been derived from the tropical forests at the eastern base of the Andes; that of the latter from the South Temperate zone plains of Argentina and Patagonia. The environmental change experienced in passing from the hot, tropical forests, at the foot of the mountains, to the cold temperate forests near their summits, is much greater than that existing between the plains of Patagonia and those of the Interandine tableland. This is obviously reflected in the degree of differentiation exhibited by the birds inhabiting these elevated forests and plains. Thus 55 per cent. of the genera of birds inhabiting the Temperate zone forests are endemic, while only 7 per cent. of the genera found on the plains of the Puna are endemic. These facts are believed to indicate that the extent of environmental change, expressed chiefly in climatic conditions, is a more important evolutionary factor than those exerted by time of isolation or extent of distance from the presumed ancestral forms.

Prof. J. P. Hill, F.R.S., V.P.Z.S., exhibited, and made remarks upon, a series of lantern-slides of some Marsupial embryos, dealing especially with the Koala (*Phascolarctos*) and the Wombat (*Phascolomys*).

PAPERS.

35. On some new Genera and Species of Anomodont Reptiles from the Karroo Beds of South Africa. By R. Broom, F.R.S., C.M.Z.S.

[Received April 6, 1921: Read May 24, 1921.]

(Text-figures 28–45.)

INDEX.

Page
Dicynodon sollasi, sp. n. 648
„ *andrewsi*, sp. n. 650
„ *osborni*, sp. n. 651
„ *watsoni*, sp. n. 653
„ *curtus*, sp. n. 654
„ *woodwardi*, sp. n. 655
„ *ictinops*, sp. n. 656
„ *macrorhynchus*, sp. n. .. 657
Bainia tigriceps (Owen), gen. n. 659
„ *peavoti*, sp. n. 659
„ *haughtoni*, sp. n. 661

Page
Eosimops newtoni, gen. et sp. n. 663
Palemydops platysoma, gen. et sp. n. 665
Emydopsis trigoniceps (Broom), gen. n. 666
„ *longus*, sp. n. 667
„ *sciuroides*, sp. n. 668
Emydops parvus, sp. n. 669
Emyduranus platyops, gen. et sp. n. 670
Endothiodon crassus, sp. n. 672

The genus *Dicynodon* was established by Owen in 1845 for the remarkable South African fossil reptiles discovered by Bain and referred to by him as Bidentals. As the result of the labours of Owen, supplemented by that of later workers, nearly every detail in the structure of the skeleton of *Dicynodon* is now as fully known as that of the Dog. It was a primitive reptile with a skeleton built essentially on the same plan as that of the mammal, but with certain remarkable specializations of the skull, especially in the complete loss of incisor teeth, the presence of a large permanently growing canine in the male, and in the fact of the front of the upper and lower jaws having formed a horny beak as in the tortoise or bird.

While there remains little to add to our knowledge of the skeleton, there is still much to be done ere we have anything like a satisfactory knowledge of the large number of species which must be referred to the genus.

Dicynodon first occurs in South Africa at the base of the *Pareiasaurus* zone, which may be regarded as Middle Permian in age, and it extends through all the zones to the top of the Permian, and forms which are very closely allied, if not indeed referable to *Dicynodon*, are met with to the top of the Trias. A form closely allied to *Dicynodon* occurs in the Dwina of Russia, and *Placerias* of the Trias of North America is, if not *Dicynodon* also, at least very closely allied.

Oudenodon, originally described as a distinct genus differing from *Dicynodon* in the absence of the tusk, we now know to be the female. So long as all the known species of *Oudenodon* differed from the known species of *Dicynodon* in other characters besides the absence of the tusk, it was felt wiser to keep *Oudenodon* as a distinct genus. In 1909, in summing up the position at that time, I stated that the evidence seemed "to be getting stronger in favour of *Oudenodon* being but the female *Dicynodon.*" By 1911 the discovery of tusked and tuskless specimens of *Dicynodon bolorhinus* in one locality removed all doubt, and since then we have discovered tusked and tuskless specimens of quite a number of species. We do not yet know whether the females of all species are tuskless, and there is considerable reason to believe they are not. And it is also possible that even the males of some species at present referred to *Dicynodon* may be tuskless. The genus *Lystrosaurus* is certainly tusked in both sexes, and as all known specimens of *Cistecephalus* are without tusks, presumably both sexes are tuskless. All the known specimens—about a dozen—of *Kannemeyeria* are tusked. Also every known specimen of *Dicynodon tigriceps* or allied species is tusked, while the few known specimens referred to *Eocyclops* are tuskless. Species where both sexes are tusked or both tuskless will have to be placed in distinct genera or at least subgenera.

When Owen worked at *Dicynodon* and *Oudenodon* he made nearly every skull the type of a distinct species, and there were doubtless many who considered that he was over liberal in the making of new species. Lydekker in 1890 reduced Owen's 20 species to 11 good and 3 doubtful species, but there is now little doubt, with our much greater knowledge of the genus, that practically all Owen's types are good. In my opinion, out of the 20 specific names only two can be regarded as synonymous—*D. pardiceps* and *D. rectidens*, both of which I refer to *D. leoniceps* Ow.

It is hardly surprising that a genus which survived for probably over 2,000,000 years should have over 50 species already known, and probably very many more to be discovered, when we consider how many species of such reptiles as *Testudo* or *Lygosoma* are at present alive. Until a few years ago nearly every good specimen discovered seemed to belong to a new species. Now the corner seems to be turned, and the majority of *Dicynodon* skulls now picked up can be referred to species already known.

In the present paper I wish to describe a number of new forms I have discovered in the past three years.

DICYNODON SOLLASI, sp. n. (Text-figs. 28, 29.)

This new species I have much pleasure in naming after Prof. W. J. Sollas, who with his daughter has added so considerably to our fuller knowledge of the structure of the *Dicynodon* skull*. It is founded on a series of over 20 good skulls and many imperfect ones discovered near Biesjespoort on a horizon which I believe to be at the very top of the *Endothiodon* zone, and it appears to extend a short way into the *Cistecephalus* zone. Though many skulls, both males and females, are known, I take as the type one of the best preserved, which I believe to be an adult male. It is about 5 inches in length and a little less than 4 inches in width.

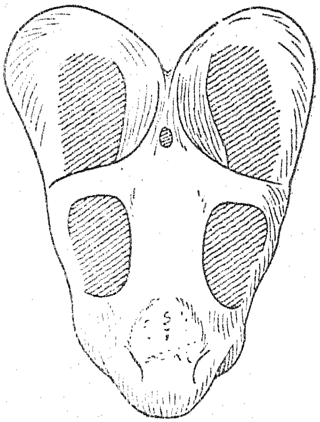
---

* In connection with the work on *Dicynodon* by Prof. and Miss Sollas, I should like to point out that the skull examined by them in 1913 cannot possibly be *Dicynodon leoniceps* Owen. As the specimen is now, of course, completely gone, and as the postorbitals have manifestly been partly weathered away before the specimen was ground down, it will never be possible to determine the species with absolute certainty. In my opinion the specimen was *Dicynodon feliceps* Owen.

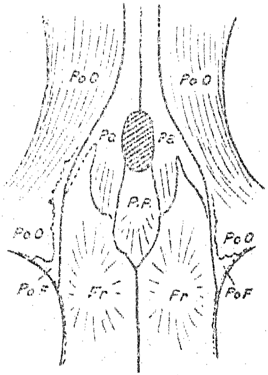
The beak is about the same length as the orbit and moderately sharp in front. The nostrils are fairly large, and behind them the maxillaries meet the nasals, and the septomaxillaries do not appear on the side of the face.

Immediately behind the plane of the nostrils is a thickening of the bones which forms a round button-like low boss in the middle line. Above and behind the canine is a thickened elongated ridge.

Text-figure 28.



Text-figure 29.



Text-fig. 28.—Skull of *Dicynodon sollasi* Broom. Reduced.
Text-fig. 29.—Preparietal region in *Dicynodon sollasi* Broom. Nat. size.

The interorbital region is flat and narrow. The orbits look upwards and outwards.

The parietal region is only very slightly wider than the interorbital, and the large postorbitals largely overlap the parietals and almost meet in the middle line.

The preparietal region is not well displayed in the type skull, but is well seen in a number of others.

The pineal foramen is relatively small, and is situated a few millimetres behind the plane of the back of the postorbital arch. The preparietal is small, and is flanked by fairly large anterior processes of the parietals. The postfrontals are nearly obscured by the parietals and postorbitals, but form a distinct though small part of the orbital margins.

The following are the principal measurements of the type skull:—

Greatest antero-posterior length	128 mm.
Width across squamosals	88 ,,
Intertemporal width	22 ,,
Interorbital width	21 ,,
Width across maxillary bosses	52 ,,
Width between nostrils	15 ,,
Width between canine roots	32 ,,

Dicynodon sollasi bears considerable resemblance to *D. feliceps*, *D. ictidops*, and *D. testudiceps*. From *D. feliceps* it differs in being a much more delicately built skull and with a very much feebler tusk, the tusk in *D. sollasi* being about half the thickness of that in *D. feliceps*. In *D. testudiceps* the postorbitals meet each other in the middle line over the parietals; in *D. sollasi* the postorbitals do not overlap the parietals so very greatly. *D. ictidops* comes from a horizon which is probably 500 feet lower than that which yields *D. sollasi*; so that there is a strong presumption in favour of the two being distinct species, though they are undoubtedly closely allied. The preparietal in *D. sollasi* is smaller than in *D. ictidops*, and the general contours of the bosses differ considerably in the two species.

DICYNODON ANDREWSI, sp. n. (Text-fig. 30.)

This species is founded on a nearly perfect skull from the same horizon and nearly the same spot at Biesjespoort that yielded the type of *D. sollasi*. In addition to the type specimen I have two others which I refer to the same species—one from a locality between Murraysburg and Biesjespoort, and the other from a locality 3 miles east of Biesjespoort. As this latter specimen was found in near association with a specimen of *Cistecephalus* sp., it gives us the horizon as the base of the *Cistecephalus* zone.

The species is a very strikingly new type, which may ultimately have to be placed in a new subgenus.

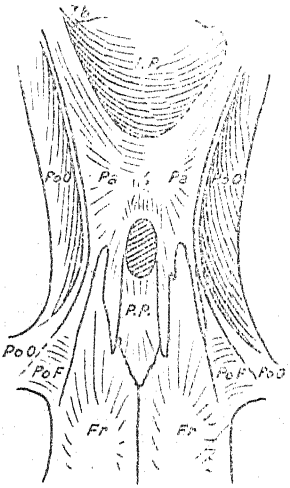
In general shape the species resembles typical Dicynodons. The snout is unusually short, the preorbital region being only about one-fifth the length of the skull. Above and behind each nostril is a well-marked bony boss, with a fairly broad flat sulcus between. Each of the two specimens which has the maxillæ preserved is tuskless.

The orbits are large, with supraorbital thickening on the frontal bones. The frontal region is slightly concave behind, and in front a low median elevation leaves each frontal bone slightly concave.

The parietal region is broad, and unlike the typical species of *Dicynodon*, the parietals are not overlapped by the postorbitals. The large size of the parietals makes a distinct approach to the broad-headed Dicynodonts of the type of *Dicynodon tigriceps* Owen, and for which I am proposing a new genus. In fact, *D. andrewsi* may be the ancestor of *D. tigriceps*.

The preparietal is well developed, and the relations of the bones in this region are very similar to the typical *Dicynodon* arrangement. There is a large postfrontal.

Text-figure 30.



Parietal region of *Dicynodon andrewsi* Broom.

The following are the principal measurements of the type:—

Greatest antero-posterior length...	about	260	mm.
Basal length	,,	210	,,
Greatest width........................	,,	230	,,
Interorbital width		43	,,
Intertemporal width		46	,,

I have much pleasure in naming the species after Dr. C. W. Andrews, F.R.S., of the British Museum.

DICYNODON OSBORNI, sp. n. (Text-fig. 31.)

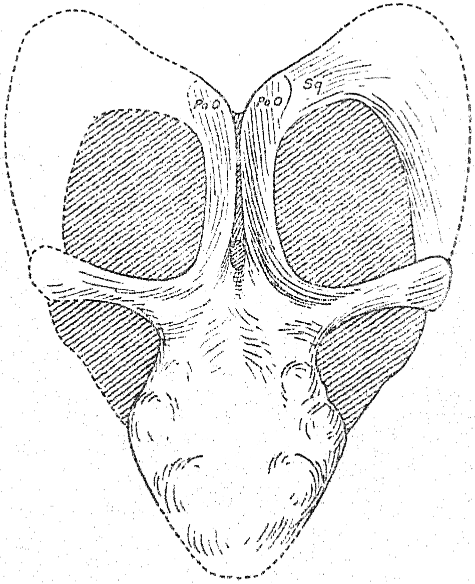
This very strikingly new species is from Wapatsberg, near New Bethesda Road, and is from beds which are undoubtedly in the *Lystrosaurus* zone. In the same horizon are found not only *Lystrosaurus*, but the Therocephalian recently described by me as *Moschorhinus kitchingi*. When *Moschorhinus* was described the exact locality was unknown to me, and when later I discovered it I made a special expedition to the spot to try and discover the back portion of the skull. Though I did not succeed in getting the rest of the type, I got another imperfect skull, two specimens of *Lystrosaurus*, and the type skull which I am now describing.

The present skull is not only of much interest as a new type, but is of great importance as being one of the very few *Dicynodon* skulls known from the *Lystrosaurus* zone, and the only known large one.

The skull lacks the lower jaw, and has lost by weathering the front of the snout, the right jugal arch and part of the left, but otherwise is fairly complete. Unfortunately, the matrix is hard, and though most of the bony surface has been displayed, it is almost impossible to be sure of the sutures.

The whole skull is broad and flat. When perfect it probably measured about 16½ inches in length, and it must have been fairly wide.

Text-figure 31.



Skull of *Dicynodon osborni* Broom. Greatly reduced.

The snout is relatively long, and apparently resembled in some respects that of *Kannemeyeria*, and as in that genus, there are a pair of very powerful tusks. The nasal region has been broad and rounded, without any very striking bony bosses.

The frontal region is wide and moderately flat. Low but well-developed bosses are above the anterior half of each supraorbital margin.

The intertemporal region is relatively narrow, and a marked median crest is formed by the flattened parietal overlapped by the large postorbitals.

The preparietal region has not been satisfactorily revealed. The pineal foramen is evidently small, and situated well back between the approaching postorbitals. Whether a preparietal bone is present or not the evidence does not show. There is certainly no preparietal boss such as occurs in the species of *Eocyclops*.

The orbits look almost directly upwards.

The postorbital arches are long and well developed.

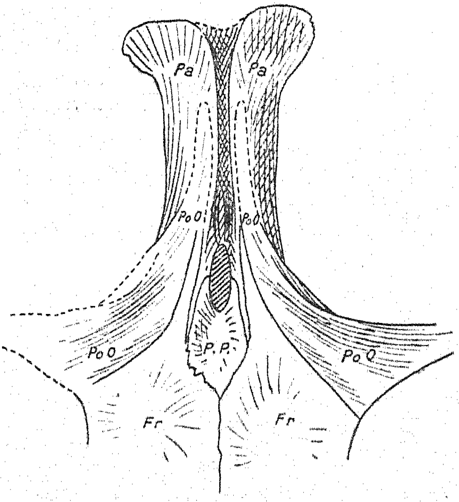
The squamosals must have been extremely broad, judging from the portions preserved.

The following are the principal measurements of the type:—

Greatest antero-posterior length...	about	460	mm.
Greatest width......................	,,	420	,,
Distance between tusks		80	,,
Interorbital width		100	,,
Intertemporal width		45	,,
Basal length	about	410	,,

I have much pleasure in naming this new type after Prof. H. F. Osborn.

Text-figure 32.



Top of parietal region of skull of *Dicynodon watsoni* Broom.
The degree to which the postorbitals overlap the parietals is unknown, but most probably it is not greater than is indicated in the figure.

DICYNODON WATSONI, sp. n. (Text-fig. 32.)

This new species is founded on a very fragmentary skull, of which little more than the frontal and parietal regions are preserved, found on the mountain to the east of New Bethesda, about 800 feet above the horizon of the village and probably in the *Lystrosaurus* zone. It is a near ally of *D. osborni* though quite a distinct species, and important in giving details of the structure of the preparietal region.

The frontal region is broad and slightly convex, and the parietal region is in the same plane as the general frontal plane. There are no supraorbital bosses as in *D. osborni*, the whole frontal surface being unusually smooth and slightly convex.

The postorbitals are large and form a considerable part of the upper cranial surface. Posteriorly they clasp the parietals, and with them form the parietal crest. Curiously enough, each postorbital has had its posterior process broken off near the plane of the pineal foramen, probably as the result of the bite of some carnivorous enemy: but there is little doubt that they extended backwards, though not so far as in typical Dicynodons, as the grooves for their lodgement are preserved. Probably, however, they did not quite extend to meet the squamosals.

The preparietal is moderately large and wide, and forms the margin of anterior third of the pineal foramen.

The postfrontal, though fairly large, is almost entirely hidden on the surface by the frontals and the postorbitals.

I have much pleasure in naming the species after Mr. D. M. S. Watson.

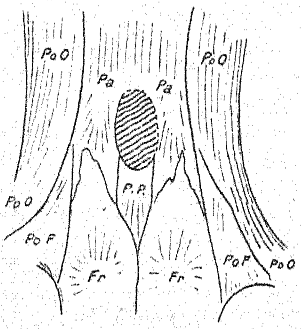
The following are the principal measurements:—

Interorbital width	58 mm.
Intertemporal width	20 ,,

DICYNODON CURTUS, sp. n. (Text-fig. 33.)

The type of this new species is a complete but distorted skull found by me at Biesjespoort. The horizon is probably about 100 feet above that in which the type of *D. sollasi* was obtained, but it is quite possible that *D. sollasi* may have survived to be contemporaneous with this other type. In any case, though this type is similar in size to *D. sollasi*, it is very strikingly different in nearly every detail.

Text-figure 33.



Preparietal region of *Dicynodon curtus* Broom. Nat. size.

The skull is short, broad, and deep, and about 4 inches in length.

The snout is bent down and the caniniform processes are under the orbits. There is no great thickening of the nasals. The orbital region is narrow and the parietal region moderately wide.

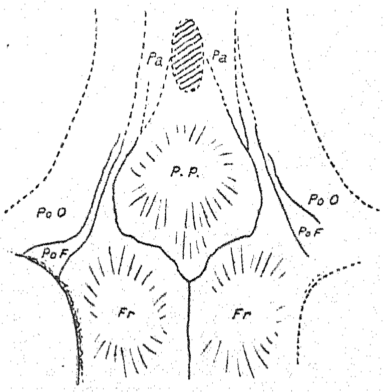
The pineal foramen is large and rounded. The preparietal is small and narrow, and the postfrontals very largely developed. The parietals are fairly well exposed between the postorbitals, but are extremely short. The postorbitals in the temporal region are broad and overhang the temporal fossæ.

The nearest ally to this species, which I propose to call *Dicynodon curtus*, is *Dicynodon dubius* Owen, from which it differs in the unusual shortness of the parietals and in other proportions.

The following are the principal measurements:—

Greatest antero-posterior length...	about	110	mm.
Greatest breadth	,,	110	,,
Basal length		100	,,
Interorbital width		20	,,
Intertemporal width		27	,,
Between the caniniform processes	about	22	,,

Text-figure 34.



Preparietal and its relations in *Dicynodon woodwardi* Broom. Nat. size.

DICYNODON WOODWARDI, sp. n. (Text-fig. 34.)

The skull which forms the type of this new species was sent to me from near New Bethesda by Mr. C. Kitching, and I am not quite sure of its horizon. Pretty certainly it is from some part of the *Cistecephalus* zone.

Though the whole of the base of the skull is preserved, much of the upper surface is unfortunately lost, including both postorbital arches with the whole of the postorbital bones, practically the whole of the parietal region, and both squamosals. Still, what is preserved shows that it is a strikingly new type, and I have much pleasure in calling it after Dr. Smith Woodward, of the British Museum.

The skull is moderately small, having measured about 6 inches in length. The snout is long and narrow, the preorbital portion of the skull being nearly as long as the postorbital. The nasal region is imperfect, but there were probably no great bony thickenings. The maxillæ have each a round tusk, the head of which lies under the orbit, and the tusks are relatively farther back from the front of the beak than in most species.

The frontals are long and moderately narrow. Behind them lies a most remarkably broad preparietal quite unlike that of any other known species. By its sides are narrow posterior processes of the frontals. The postfrontals lie outside the frontal processes. The postorbitals are lost, but from the condition of the posterior parts of the squamosal it is manifest that the temporal region must have been comparatively narrow.

The following are the principal measurements:—

Greatest antero-posterior length... about	160	mm.
Greatest breadth .... perhaps about	110	,,
Basal length	145	,,
Interorbital width	30	,,
Distance between tusks	29	,,

DICYNODON ICTINOPS, sp. n. (Text-fig. 35.)

This new species is formed on the nearly perfect skeleton of a small animal found by me about 30 miles from Biesjespoort on the Murraysburg Road. While it is quite possible that the form is not quite fully grown, it cannot be the young of any known species.

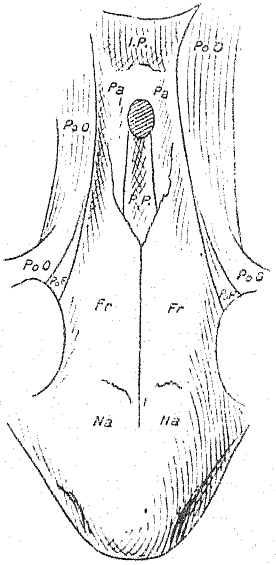
The head is about 3¼ inches in length, and the whole animal from snout to the tip of the tail about 12½ inches.

The snout is smooth and rounded, without any bony thickening either on the nasals or in the supraorbital regions, except a very slight thickening on the nasal just where it overhangs the nostril. The septomaxillary does not appear to show on the face. The lacrimal and prefrontals are small. In the maxillæ is a small tusk.

The frontals are large, and a transverse section in the orbital region would show a convex upper surface, while a section of the posterior end would have a concave upper surface. The postfrontals are small, and only a small part appears on the surface. The preparietal is rather small, its anterior end being on the plane of the postorbital arch. The pineal foramen is situated far back. The parietals are small. The postorbitals are very large, and their posterior processes are kept apart farther than in most *Dicynodon* species.

On some future occasion the skeleton will probably be described in detail. For the most part the bones are surrounded by very hard calcareous masses, and are very difficult to clear.

Text-figure 35.



Top of skull of *Dicynodon ictinops* Broom.

The following are the principal skull-measurements:—

Greatest antero-posterior length	82	mm.
Greatest breadth	68	,,
Interorbital width	18	,,
Intertemporal width	19	,,
Basal length	about 70	,,
Distance between canines	15	,,

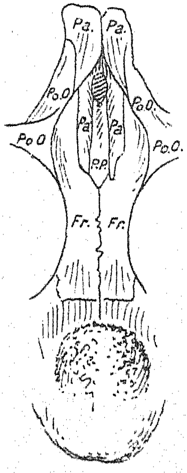
DICYNODON MACRORHYNCHUS, sp. n. (Text-fig. 36.)

This new species is founded on two small skulls discovered by me at New Bethesda. For a time I considered they might be very miniature specimens of *Dicynodon platyceps*, the common New Bethesda species, but further careful examination shows that it is necessary to regard them as belonging to a distinct species. The best preserved specimen is taken as the type.

The skull when complete was considerably less than 3 inches in length, and if an adult it represents one of the smallest known species of *Dicynodon*. It is chiefly remarkable for the great length of the orbital and preorbital regions as compared with the postorbital.

In the nasal region there is a large median thickening resembling that in *Dicynodon sollasi*. The frontal region is narrow and the orbits large. The postorbital arch is slender and the postorbital bones are quite unusual in shape. There is no trace to be seen, at least on the upper surface, of any postfrontal, and the postorbital takes its place, having an anterior process which forms a considerable part of the supraorbital margin. The posterior process is unusually short, much of the temporal wall being formed by the parietal. The pineal foramen is of moderate size, and is situated as shown in the figure given. The preparietal is long and narrow.

Text-figure 36.



Top of skull of *Dicynodon macrorhynchus* Broom.

The posterior portion and much of the palate are crushed.

The following are the principal measurements:—

Greatest length	probably about 70	mm.
Interorbital width	7·5	,,
Intertemporal width	8	,,
From snout to front of pineal foramen...	47	,,

Dicynodon macrorhynchus is allied to *D. sollasi*, *D. testudiceps*, and *D. ictidops*, but being from the middle of the *Cistecephalus* zone, must be from a horizon many hundreds of feet higher than that of any of these others.

BAINIA TIGRICEPS (Owen), gen. n.

One of the first species of *Dicynodon* to be described by Owen was *Dicynodon tigriceps*. This is represented in the British Museum by a very fine skull, said to have come from "Gonzia River, Kaffraria." In general appearance it differs very considerably from the typical *Dicynodon* as represented by *D. lacerticeps*. The skull is massive and extremely broad and flat, and the parietal region differs in that the parietals are well developed and not covered by the postorbitals. The genus *Dicynodon* is so large that it would be convenient if we could lop off a few species and put them into a subgenus, even if the differentiating characters did not seem of very fundamental importance. But there is another character that is of great importance. I know of nine skulls which belong either to *Dicynodon tigriceps* or closely-allied species, and all have tusks. It is therefore very highly probable that the female of *Dicynodon tigriceps* was tusked, and not like the female *Dicynodon*—tuskless. And if this be so, *Dicynodon tigriceps* must be placed in a distinct genus. It is, of course, impossible to prove that the female was tusked, and even if 50 tusked skulls were found there would still be a doubt. As it is, I think the probability sufficiently great to make for it a new genus, *Bainia*, after the father of South African geology, Andrus Geddes Bain—one of the most gifted geological geniuses the world has seen. Even if a tuskless female should turn up, *Bainia* must still stand as a subgenus.

BAINIA PEAVOTI, sp. n. (Text-fig. 37.)

This new species is founded on a very fine skull discovered by me at Biesjespoort. The skull is well preserved and not much crushed. One zygomatic arch is lost, also part of the base and the lower jaw. Though very similar in size to *Bainia tigriceps*, it differs in many important features; and as it is manifestly a new species, I have much pleasure in naming it after the late Henry G. Peavot, who for some years was the Zoological Society's Librarian and Clerk of Publications, and whose care and kindly help all workers so fully appreciated. It is a delight to be able to add a stone to the cairn of a fellow-worker and friend who laid down his life on the battlefield.

The skull is of special value in that all the sutures can be made out with perfect distinctness. In general shape it agrees more closely with *B. tigriceps* than with *B. laticeps*, but differs in the shape of the zygomatic arch and in many other details which will be mentioned. The snout and the whole front half of the skull is much flatter than in any other known Anomodont.

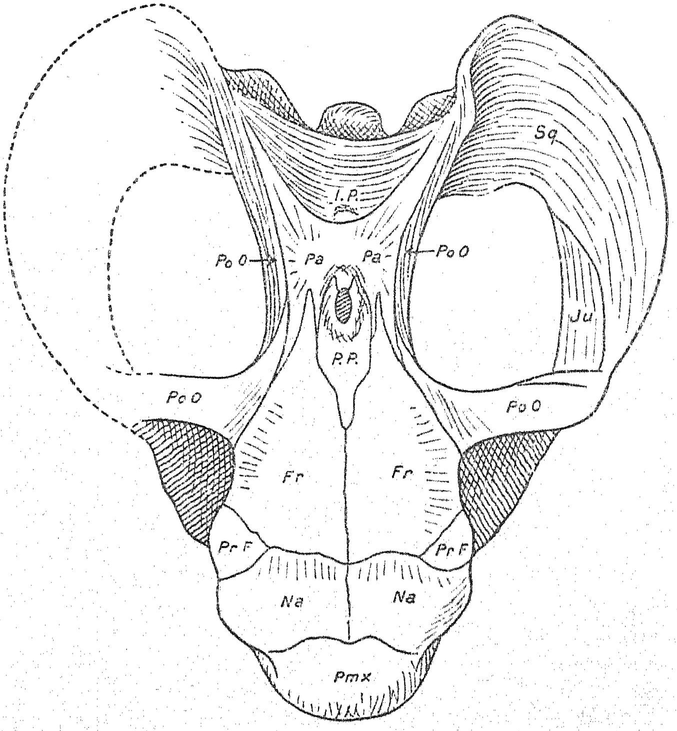
The premaxilla, which is nearly complete, is relatively small and unusually flat.

The nasals are short but very broad, and have each a well-developed boss which overhangs the nostril. The suture with the frontals and prefrontals is nearly transverse.

The septomaxilla is not satisfactorily preserved, but is relatively small.

The maxilla is a very remarkable bone, quite unlike that in any other known Dicynodont. The bone of the left side has lost the subnasal portion, but is otherwise nearly complete, and it is so remarkably shallow that one would fancy the palatal half had been removed; yet if part of the bone has been removed, it must have been done during the animal's lifetime. There is no trace of a tusk, yet there are the remains of the socket of a large tusk. A not improbable explanation of the peculiarity is that the animal is aged and has lost its tusks, and that in consequence the palatal portions of the bone have become absorbed, as is seen in aged human and other mammalian jaws.

Text-figure 37.



Skull of *Bainia peavoti* Broom.

The prefrontal is a relatively small trianguar bone which has a small and not very prominent boss above the front of the orbit.

The lacrimal is small.

The jugal is large. It forms most of the lower border of the orbit, most of the postorbital arch, and a considerable part of the zygomatic arch.

The frontal is unusually large and wide. Its shape will be best understood from the figure given. It has apparently a large articulation with the postorbital, but a thin little strip of the postfrontal is really wedged in between them. The frontal passes back to the plane of the posterior end of the pineal foramen.

The postfrontal scarcely appears on the surface, but though nearly hidden by the frontal and postorbital, it is really a bone of appreciable size underneath.

The postorbital is a large and powerful bone. It forms most of the strong postorbital arch and the whole of the upper border of the temporal fossa, and pretty certainly articulates with the squamosal.

The preparietal is unusually large. It passes far forwards between the frontals, and posteriorly nearly surrounds the pineal foramen.

The parietals appear to be ankylosed into a fairly large bone lying mainly behind the pineal foramen. It forms a moderately large, somewhat concave intertemporal region. Anteriorly it sends forward on each side a slender process between the frontal and postorbital, and posteriorly a long process between the postorbital and interparietal.

The interparietal is a little broader than the middle part of the parietal. Laterally it articulates with the large tabular.

The occiput is fairly well preserved, and was probably much like that of *Bainia tigriceps*, though some degree of crushing of the squamosals gives it a rather different appearance. The occipital condyle is much shorter in the present species.

The squamosals are, as in all Dicynodonts, large and powerful. The shape of the zygomatic portion can be seen in the figure to differ appreciably from that in *B. tigriceps*.

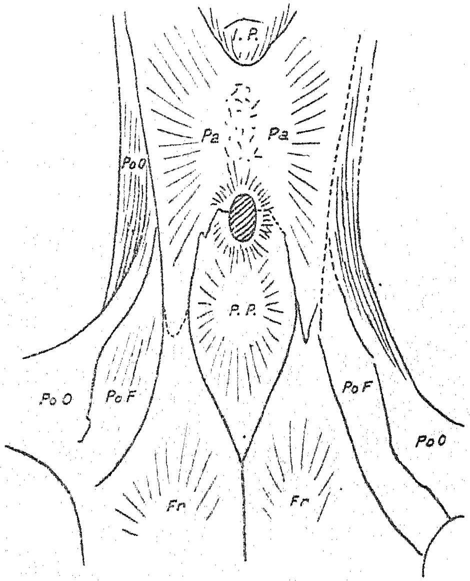
The following are some of the principal measurements :—

Greatest length (oblique)	500 mm.
Greatest breadth	480 ,,
Basal length	400 ,,
Width across nasal bosses	163 ,,
Interorbital width	133 ,,
Intertemporal width across parietals...	50 ,,
Intertemporal width across postorbitals..................................	86 ,,

BAINIA HAUGHTONI, sp. n. (Text-fig. 38.)

In Haughton's paper on the Anomodonts in the South African Museum, recently published, he figures and describes a skull (S. A. M. No. 3328) which he believes to be a young specimen of *Dicynodon laticeps*. I have examined this skull, and while it has all the appearance of a young skull, it cannot, in my opinion, be the skull of a young *D. laticeps*, as it differs in having a very large preparietal and very large postfrontals. Nor can it be the young of either *Bainia tigriceps* or *D. peavoti*. And as it differs from all these three species, but manifestly belongs to this group, it is necessary to make it the type of a distinct species which I have much pleasure in naming after Mr. S. H. Haughton, who is doing excellent work in the vast South African field.

Text-figure 38.



Parietal, preparietal, and frontal regions of *Bainia haughtoni* Broom.

Mr. Haughton, in addition to describing the specimen, has given a figure of the preparietal region. While his figure is essentially correct, a camera lucida drawing I have made of this region gives, I think, a little more accurately the position of the sutures.

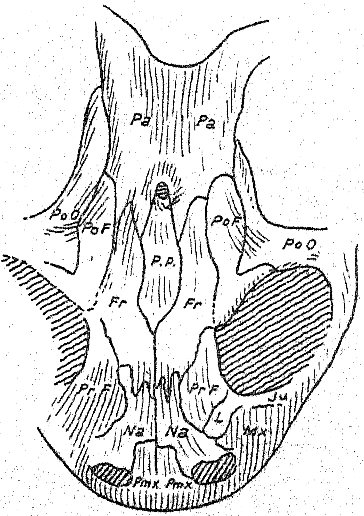
The following are some of the principal measurements:—

Interorbital width	46 mm.
Intertemporal width	34 ,,
Across the nasals	52 ,,
Between the canines .... about	50 ,,

Eosimops newtoni, gen. et sp. n. (Text-fig. 39.)

This genus and species is founded on a skull which I discovered at Victoria West, and which is of special importance as throwing some light on the age of the rocks which yielded the unique fossil forms *Galechirus scholtzi*, *Heleosuchus scholtzi*, *Arnognathus parvidens*, and *Heleophilus acutus*. When these fossils were discovered by Mr. Scholtz no other fossil had been found within 40 or 50 miles, and there was much doubt as to the age of the deposit. When I described the forms I thought it very likely that they were some of the land representatives of the *Lystrosaurus* zone. Shortly afterwards Mr. A. L. du Toit, of the Geological Survey, reaching Victoria West from the north through a very unfossiliferous region, came to the conclusion that the beds at Victoria West were probably of the *Pareiasaurus* zone. For many years I have taken Mr. du Toit's opinion, but working from the South I have been compelled to differ. Biesjespoort, which lies about 20 miles south of Victoria West, is very rich in fossils, and is certainly at the base of the *Cistecephalus* zone. For miles the strata are almost perfectly horizontal, and it is hard to believe that the beds at Victoria West can be much lower than those at Biesjespoort. Unfortunately, the intermediate beds so far as examined are almost

Text-figure 39.



Skull of *Eosimops newtoni* Broom.

The apparent asymmetry is partly due to crushing, but largely owing to different degrees of the surface of the bones having been flaked off.

devoid of fossils till we come to the little rich patch at Victoria West. Soon this locality will be for ever drowned in a large dam which is being made above the township.

A small Dicynodont skull was some years ago discovered in the deposit, which I referred to *Pristerodon mackayi* Huxley, and took this as confirmatory evidence of the deposit being in the *Pareiasaurus*-zone; but we now know that very similar forms belonging to the genus I am calling *Emydopsis* occur in the *Cistecephalus* zone.

The new Dicynodont skull which I have discovered is nearly perfect, but being in a hard matrix cannot be very satisfactorily developed. It is about 5 inches long and 4 broad, and is chiefly remarkable from having the preorbital region very short and deflected and the parietal region very broad.

The premaxilla is extremely small and short. The nostrils are large and directed forwards. The nasals, like the premaxilla, are also unusually small. The septomaxilla does not show on the facial surface. The maxilla though fairly well developed is very short. It has a rather small slightly flattened tusk.

The prefrontal and lacrimal are both small. The frontals are long and narrow, and form only a small part of the orbital margin. Between them lies an exceptionally large and long preparietal. The postfrontals are also very large. The postorbitals, on the other hand, have very short posterior processes which do not meet the squamosals. The parietals are well developed and broad.

The pineal foramen is unusually small.

The squamosal does not seem to present any unusual features.

The occiput has not been cleaned of matrix.

The species in the folding down of the snout recalls *Lystrosaurus*, though the narrow interorbital region gives the upper surface quite a different appearance. In *Dicynodon moschops* Broom we have a very similar folding down of the snout, and at first sight one might be led to think that this skull was the male of *D. moschops*. When, however, we look at the structure we find very great differences. In *D. moschops* we find the septomaxillary large and forming part of the face. Here it does not appear on the face. Further, in *D. moschops*, though the parietals are also broad the preparietal is small, and there are no postfrontals showing on the upper surface. The species of *Bainia* also show some affinities with the present type, but they all differ in having the frontal region broader than the parietal. Still we may conclude that this Victoria West type has affinities with *D. moschops* on the one hand and with the species of *Bainia* on the other. As all the known species of *Bainia* occur in the *Cistecephalus* zone, as does also *D. moschops*, we may, I think, conclude that the Victoria West animal is either from the *Cistecephalus* zone or from the zone immediately below—viz., the *Endothiodon* zone. In any case it is pretty certain that the Victoria West deposit cannot belong to the *Pareiasaurus* zone.

It is certainly very remarkable that, while we know the faunas of the *Endothiodon* and *Cistecephalus* zones fairly well, nowhere else have we ever come across any of the forms that occur at Victoria West.

Though the present Dicynodont is fairly new to the typical Dicynodons, I think it well to make it the type of a new genus, which may be called *Eosimops*, characterized by the very short deflected snout and the broad and unusual condition of the parietal region. The specific name has been given in honour of Mr. E. T. Newton, F.R.S., whose work I have always greatly admired.

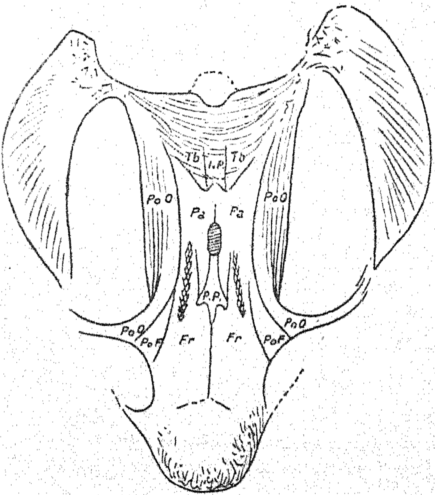
The following are the principal measurements:—

Greatest antero-posterior length...	about	140 mm.
Greatest breadth	,,	100 ,,
Interorbital width		30 ,,
Intertemporal width		33 ,,

PALEMYDOPS PLATYSOMA, gen. et sp. n. (Text-fig. 40.)

This new genus and species is founded on a beautiful skull and part of the skeleton of a small Dicynodont found by me at Biesjespoort. The head is barely 3 inches long, and one might consider the possibility of its being a young *Dicynodon*. But this cannot well be the case, as the bones are well ossified and the tusk apparently fully formed. Further, the structure of the top of the skull is unlike that in any known species of *Dicynodon*.

Text-figure 40.



Skull of *Palemydops platysoma* Broom.

In fact, the top of the skull differs so greatly from that of typical Dicynodons, that I feel justified in making the specimen the type of a new genus, *Palemydops*.

The skull is flat and broad. The snout is very short. There are no indications of any thickenings of the nasal bones. The maxilla is short and has a well-developed round tusk. The sutures of the snout elements cannot with certainty be made out.

The frontals are moderately broad, and on the back part of each is a long deep, probably glandular pit. The postfrontals are large, and form a considerable part of the orbital margin. The postorbitals are very large, and form the whole of the inner wall of the temporal fossa.

The preparietal is relatively small and narrow. The pineal foramen is small, and lies much behind the plane of the post-orbital arches. The parietals are large.

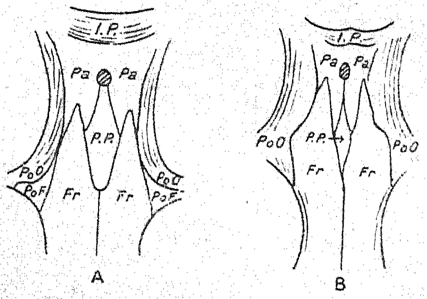
The following are the principal measurements of the skull:—

Greatest antero-posterior length	75	mm.
Greatest width..............................	67	,,
Interorbital width	16	,,
Intertemporal width	20	,,

EMYDOPSIS TRIGONICEPS (Broom), gen. n. (Text-fig. 41 A.)

In 1904 I described a small Anomodont skull as a species of *Oudenodon* and called it *Oudenodon trigoniceps*. With the much greater knowledge which we now have it became pretty manifest that it could not be a species of *Oudenodon*, or rather of *Dicynodon*, the parietal region being quite different from the *Dicynodon* type. The specimen is now in the Albany Museum, and Mr. J. Hewitt, the Curator, kindly sent it to me on loan for further examination. I discovered on breaking into the maxilla that there are three or four slender molar teeth. These are long

Text-figure 41.



A. Preparietal region of *Emydopsis trigoniceps* Broom.
B. Preparietal region of *Emydopsis sciuroides* Broom.

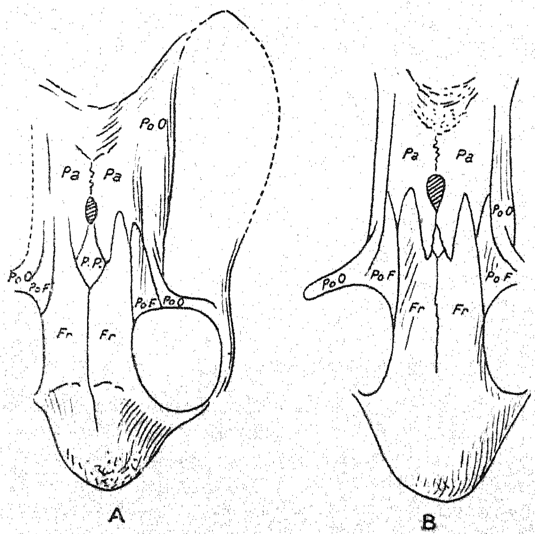
and rounded, and with small serrations on the posterior side of the upper portions of the crowns. Manifestly the genus is allied to *Pristerodon* and to *Emydops*, and also to *Dicælurodon*, but it seems wisest to make a new genus for those forms with three or four slender posteriorly serrated teeth. *Pristerodon* has a larger number of molars—6, 7, or 8—and they are robust teeth. *Emydops* has a few teeth which are apparently not serrated. *Dicælurodon* has a number of molars which have serrations both in front and behind.

Emydopsis trigoniceps (Broom) may be taken as the type species of the new genus.

EMYDOPSIS LONGUS, sp. n. (Text-fig. 42.)

This species is founded on a collection of eight good and a number of imperfect skulls found by me at Biesjespoort. They occur in exactly the same horizon as *Dicynodon sollasi*. As most of the skulls are about 2$\frac{1}{2}$ inches in length, and no one is more than 2$\frac{3}{4}$ inches, we may safely conclude that they are adult skulls.

Text-figure 42.



Skulls of *Emydopsis longus* Broom.

A. Type skull.

B. Skull of a topotype illustrating the variability of the preparietal.

The snout is very appreciably shorter than the antero-posterior diameter of the orbit. It is above rounded and moderately smooth, though the nasal bones are uniformly thickened. The septomaxillary does not seem to be seen on the face, though it is impossible to be quite certain.

The frontals are long and narrow, and nearly shut out from the orbital margins by the præfrontals and large postfrontals. They pass far backwards by the sides of the preparietal. The frontals are moderately flat.

The preparietal differs in different specimens considerably, but the appearance of the postfrontals, postorbitals, and parietals is very constant. I give figures of the region in two specimens to illustrate the variation.

The parietals are large and broad and flanked by the postorbitals.

In no specimen is there a tusk, but in both upper and lower jaws are a few slender posteriorly serrated molars. The number appears to vary with age. In a beautifully preserved lower jaw there are three teeth. The first is large and is on the point of being shed, the replacing tooth being seen below it. The second tooth is also well developed. The third tooth is very small.

A few years ago Haughton and I described a small skull from Dunedin, which we provisionally referred to *Emydops* and named *Emydops platyceps*. There can be little doubt that this is very closely allied to the present species, and should be transferred to the genus *Emydopsis*.

The only striking difference between *Emydopsis platyceps* and *Emydopsis longus* is that in the latter the posterior part of the skull is much longer and broader, and while *E. platyceps* has slender tusks, *E. longus* has none.

The following are the principal skull measurements (in millimetres) of three specimens:—

	Type.	B.	C.
Greatest length	64	68	72
Greatest width ...... about	48	about 54	about 52
Interorbital width	12	11	12
Intertemporal width	18	18	20
Basal length	59	about 62	—

EMYDOPSIS SCIUROIDES, sp. n. (Text-fig. 41 B.)

The beautiful little skull which forms the type of this new species was found by me at New Bethesda, the famous locality which has already yielded so many interesting types. Without seriously injuring the skull, it will not be possible to say with certainty if the specimen belongs to *Emydopsis*, but the general resemblance of the skull and lower jaw to those of species of *Emydopsis* is so close as to render it highly probable that the specimen belongs to a species of this genus.

The next striking characteristics of the skull are the large size of the orbit and the relative shortness of the parietal region.

The snout is short but relatively broad. A tiny corner of the septomaxillary appears on the face. The maxilla is deep, and in this type skull at least, tuskless. The prefrontal and lacrimal are small.

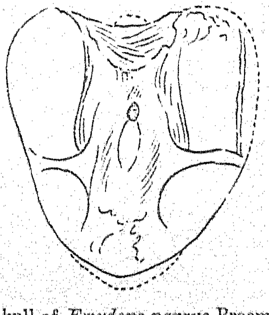
The frontal is very long and narrow, and remarkable in that the postorbital portion is wider than the orbital. The preparietal is almost unique among Anomodonts in being very small and situated entirely in front of the pineal foramen. A similar condition is only known to occur in *Emydopsis arctatus* (Owen). The postfrontal is either entirely absent or does not appear on the surface. The postorbital is very large, and extending forward into the region usually occupied by the postfrontal, forms a considerable part of the orbital margin. The parietal is moderately wide but short, the part behind the pineal foramen being extremely short. The pineal foramen is very small.

In the lower jaw the dentary resembles that of *Emydopsis longus*, but the post-dentary portion of the jaw is relatively much shorter.

The following are the principal measurements of the skull :—

Greatest length	about	60	mm.
Greatest width	doubtfully about	50	,,
Interorbital width		10	,,
Intertemporal width		17	,,
Between caniniform processes		11	,,
Basal length	about	48	,,

Text-figure 43.



Skull of *Emydops parvus* Broom.

The skull is slightly crushed, but could not well have been longer than indicated by the dotted line.

EMYDOPS PARVUS, sp. n. (Text-fig. 43.)

Until the discovery of the present specimen, *Emydops minor* was the smallest known Anomodont, but this new find gives us a type which has certainly a shorter skull and possibly smaller in other respects. This new species is founded on a skull discovered by me at Bruintjeshoogte in the same stratum as yielded the type skull of *Ictidosuchus longiceps* Broom.

The skull is $1\frac{1}{2}$ inches long and rather less in breadth, and the whole animal was probably as small as a newly-born kitten.

The snout is very short, but the structure cannot be made out owing to crushing.

The orbits are small.

The frontal region is relatively narrow, and the temporal region in front nearly twice as wide. Owing to a finely crackled condition of the bones, sutures are very difficult to make out, but the limits of the preparietal can be clearly seen. The pineal foramen is small and situated well back. The general shape of the skull will be best indicated by the drawing given.

There is evidence of at least one small unserrated molar.

The following are the principal measurements of the skull:—

Greatest length....................	about	38 mm.
Greatest breadth		35 ,,
Interorbital width		8·5 ,,
Intertemporal width		22·5 ,,

EMYDURANUS PLATYOPS, gen. et sp. n. (Text-fig. 44.)

The new genus and species is founded on a small skull discovered by me near Biesjespoort, and is one of the most interesting Anomodonts known. The specimen was found in the deposit which has yielded the very numerous skulls of *Dicynodon sollasi*, and before being developed it was looked upon as another of the many duplicates. This was unfortunate, for a beautiful shoulder-girdle lying against the skull was developed out and a portion of the skull sacrificed before it was noticed that the skull is really a very remarkable new type. We have still preserved the greater part of the skull, minus the arches, but with the contact between the occiput and the parietal region lost.

The skull is that of a small Anomodont with a broad, flat head and a wide palate which has on each side three or four teeth.

The premaxilla is broad and shallow. As in typical Anomodonts, it forms the greater part of the bony palate. There is a well-marked median ridge. Its relation to the palatines and maxillæ will be best understood by the figure.

The maxilla is well developed, but is remarkable from the fact that there is very little of a caniniform process. Some distance inside of the alveolar margin are three or four teeth in a row. On the right side the matrix has been left supporting the crowns. The first is a small sharp-pointed unserrated tooth; the second a much broader flattened tooth, also without serrations; the third probably similar to the second; and the fourth a smaller tooth imperfectly preserved. On the left side the matrix, and with it much of the teeth, has been removed. The first tooth is seen to have its root near the suture between the premaxilla and maxilla, and though it doubtless is fixed in the maxilla, it passes through the premaxilla. The others are in the posterior part of the maxilla.

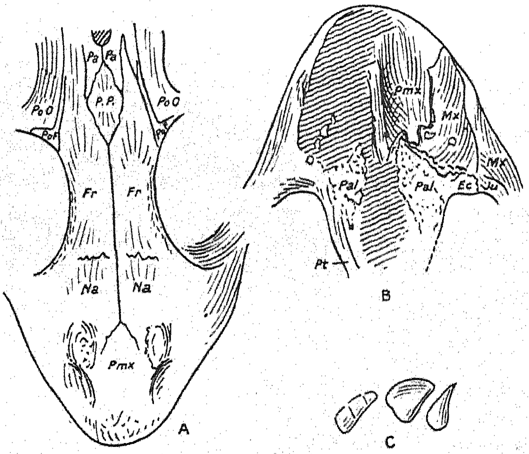
The palatine is well developed and has an unusually large palatal portion, which is rugose and has probably had a horny protection. The posterior part of the palate is not preserved.

The nostrils are situated well forward and separated by the median process of the premaxilla, which passes well back.

The nasals are large. Each has a well-marked boss behind and above the nostril. The septomaxillæ cannot be made out.

The frontal is long and narrow, and passes unusually far behind the plane of the postorbital arch. The postfrontal is small and narrow, but forms a considerable part of the orbital margin.

Text-figure 44.



A. Top of skull of *Emyduranus platyops* Broom.
B. Palate of *Emyduranus platyops* Broom.
C. First three molar teeth of same, enlarged.

The preparietal is remarkable in being situated quite in front of the pineal foramen. It is lozenge-shaped, the two posterior sides articulating with the parietals and the anterior with the frontals.

The postorbitals are large.

The occiput, so far as can be seen, presents no unusual feature.

The following are the principal measurements :—

Greatest length	about	90 mm.
Greatest width		72 ,,
Interorbital width		16 ,,
Intertemporal width		20 ,,
Between the caniniform processes		25 ,,
Front of snout to front of pineal foramen		62 ,,

This little Anomodont, to which I have given the name *Emyduranus platyops*, shows some affinities with *Cryptocynodon simus* Seeley, and also with *Prodicynodon pearstonensis* Broom, but must be regarded as the representative of a very distinct genus.

ENDOTHIODON CRASSUS, sp. n. (Text-fig. 45.)

This new species is founded on a beautiful skull discovered by me at Dunedin, Beaufort West district. The skull has lost the lower jaw, and has the parietal region badly weathered and the squamosal portion of the left temporal arch imperfect, but otherwise it is almost complete. With the exception of *Endothiodon whaitsi* it is the largest *Endothiodon* skull known, and it is little inferior to that other, though very different in shape.

Unlike *Endothiodon uniseries* Owen and *Endothiodon whaitsi* Broom, it is very broad and flat, and the parietal region is only slightly elevated above the frontal plane. In general shape and proportions the species which it most resembles is *Endothiodon paucidens* Broom, but that it is very different from this species will be at once evident on comparing the figures.

The premaxilla when viewed from the front is like a thick inverted **V**, the deep notch being for the point of the mandible, and the two points are the caniniform processes, which here are formed by the premaxilla and not, as in the tuskless Dicynodonts, by the maxillæ. A small knob is situated in front of each nostril. The superior median process passes between the nasals, but is short.

The nasals are very broad, and the bones, like all the bones of the top of the skull, very thick. They are as broad as long, and the whole preorbital portion of the skull is thus much broader than long—a condition which differentiates this species of *Endothiodon* from all others.

The prefrontals are of moderate size, and so thickened that they may be looked upon as forming preorbital bosses.

As in all typical Endothiodons, there are two longitudinal grooves passing from the front of the frontals down the middle of the nasals to the upper corners of the nostrils.

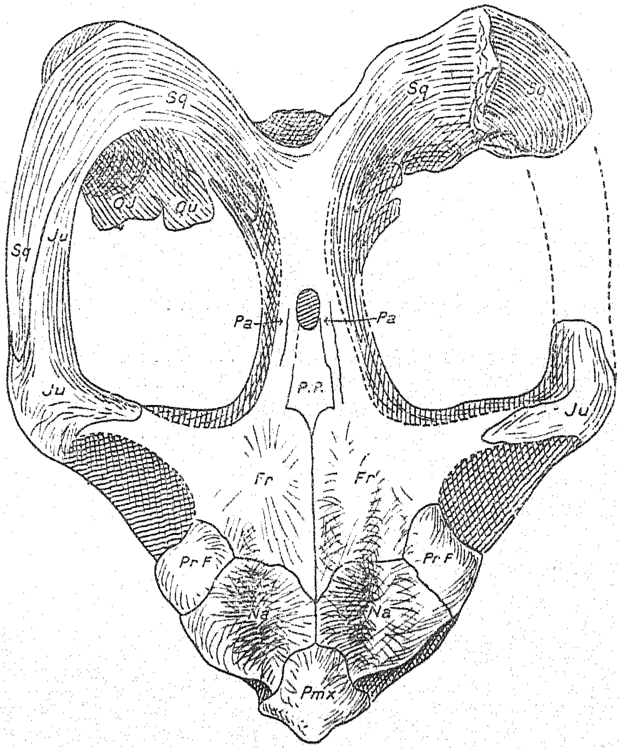
The septomaxilla seems to be small and within the nostril, but the evidence is not satisfactory as to whether it also appears on the face.

The lacrimal is smaller than the prefrontal, but its limits cannot be clearly made out.

The maxilla is a large bone. As in all species of *Endothiodon*, it has a long ridge which forms an alveolar border and at a considerable distance further in a row of teeth. Most of the teeth appear to be lost, but when complete there was probably a single row of eight teeth which measured 74 mm. The first tooth of the series is round in section and has a diameter of 7 mm.; the last, also round, has a diameter of 8·5 mm. The maxilla forms most of the lateral part of the face, and it sends a long and powerful process outwards and slightly backwards below the jugal to strengthen the jugal arch.

The jugal is, as in other Endothiodonts, more powerful than in the Dicynodonts, and has a large rounded descending knob. It sends a long process backwards inside the squamosal.

Text-figure 45.



Skull of *Endothiodon crassus* Broom. Greatly reduced.

The quadrato-jugal and quadrate (*QJ* and *Qu*) of the right side are displaced: those of the left side lost.

The frontals are large, but the exact limits of the bones cannot be made out except in front as most of the orbital margins have been lost.

The preparietal is large and forms the front of the pineal foramen wall.

The parietals are narrow but deep.

The squamosals are powerful. The zygomatic portion is more slender than in Dicynodonts, but the occipital portion is greatly developed.

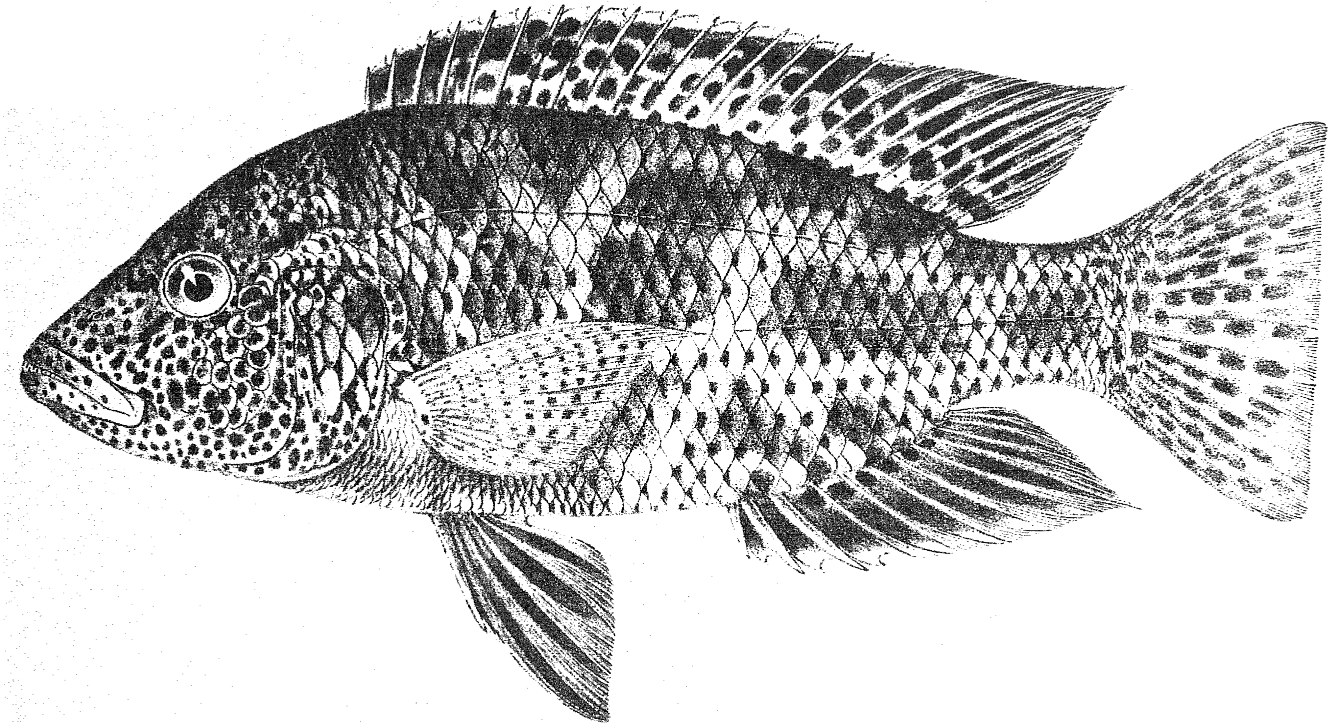
The quadrate and quadrato-jugal are lost from the left side, but preserved in a slightly displaced condition on the right. As in *Dicynodon*, they are apparently ankylosed, and their displacement from the squamosal and paroccipital adds further evidence to observations I have made in *Dicynodon*, that while the quadrate is fixed to the quadrato-jugal, the quadrato-jugal has a very considerable degree of movement on the squamosal, and thus relatively to the skull the quadrate is perhaps as freely movable as in the Lizard, in Anomodonts, and also in Cynodonts.

The palate is similar to that in other Endothiodonts, and does not differ greatly from the *Dicynodon* type. The periotic processes do not descend to the same degree as in *Dicynodon*, but are clasped by the basisphenoids in a similar manner, and have each a large foramen ovale for the end of the stapes. *Endothiodon* differs from *Dicynodon* in having a large median basisphenoid boss.

The occipital condyle is flat as in other *Endothiodon* species.

The following are the principal measurements of the skull :—

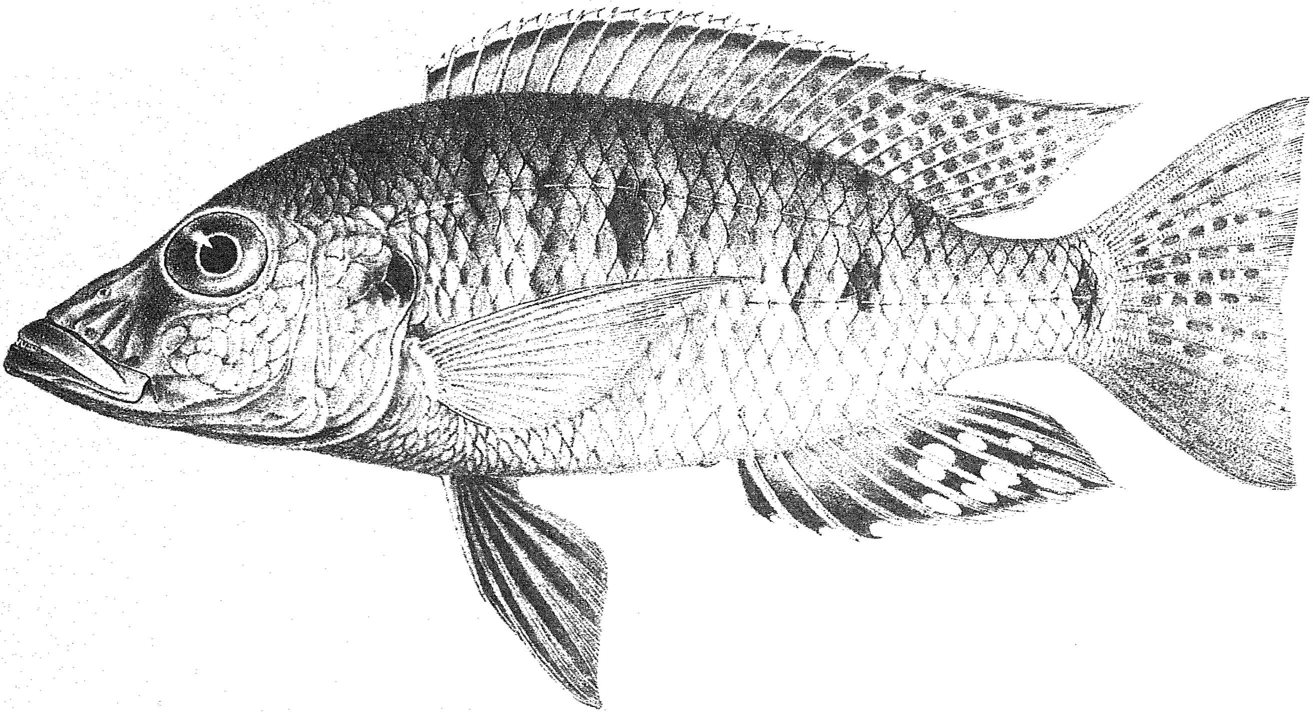
Greatest antero-posterior length......	502	mm.
Greatest breadth across squamosals....	400	,,
Greatest breadth across jugals........	430	,,
Breadth across nasals	180	,,
Breadth between nostrils............	60	,,
Basal length	435	,,



J. Green del. et lith.

Huth imp.

HAPLOCHROMIS POLYSTIGMA 4/5.

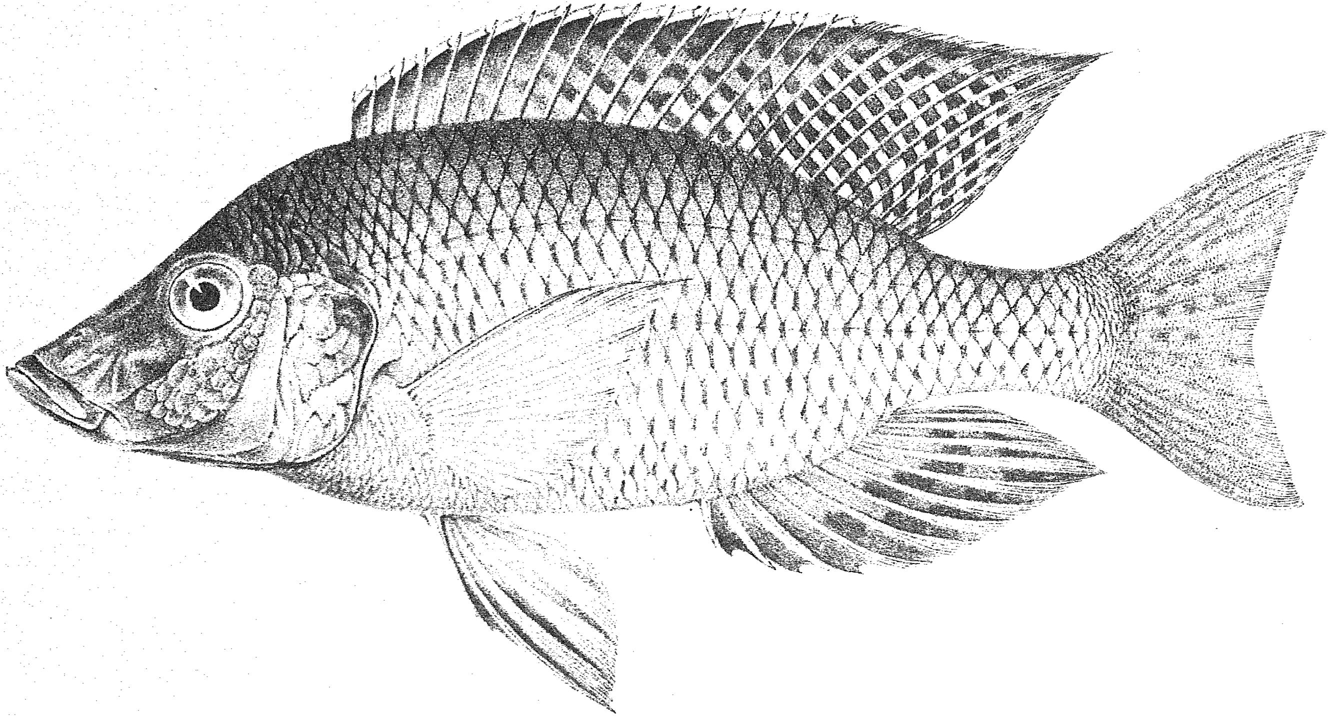


J. Green del. et lith.

Huth imp.

HAPLOCHROMIS WOODI. 4/5.

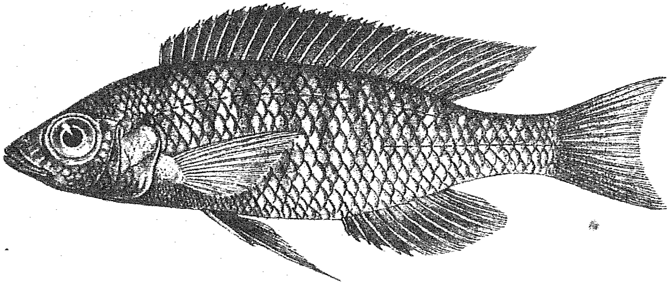
P. Z. S. 1921. REGAN. Pl. III.



J. Green del. et lith.

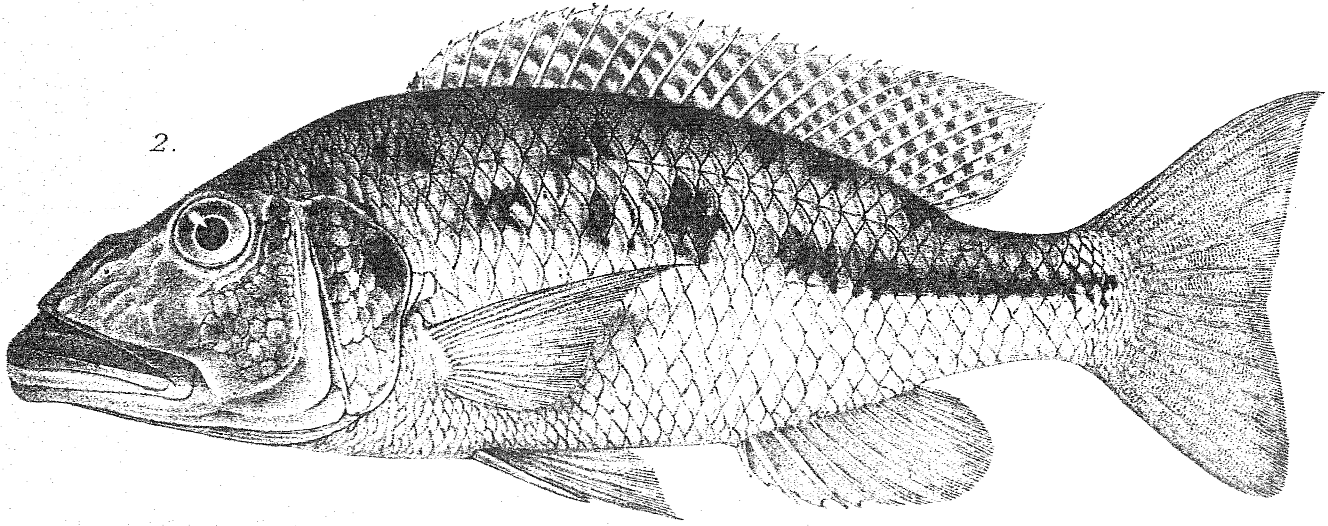
Huth imp.

HAPLOCHROMIS PRÆORBITALIS, 3/4.



1.

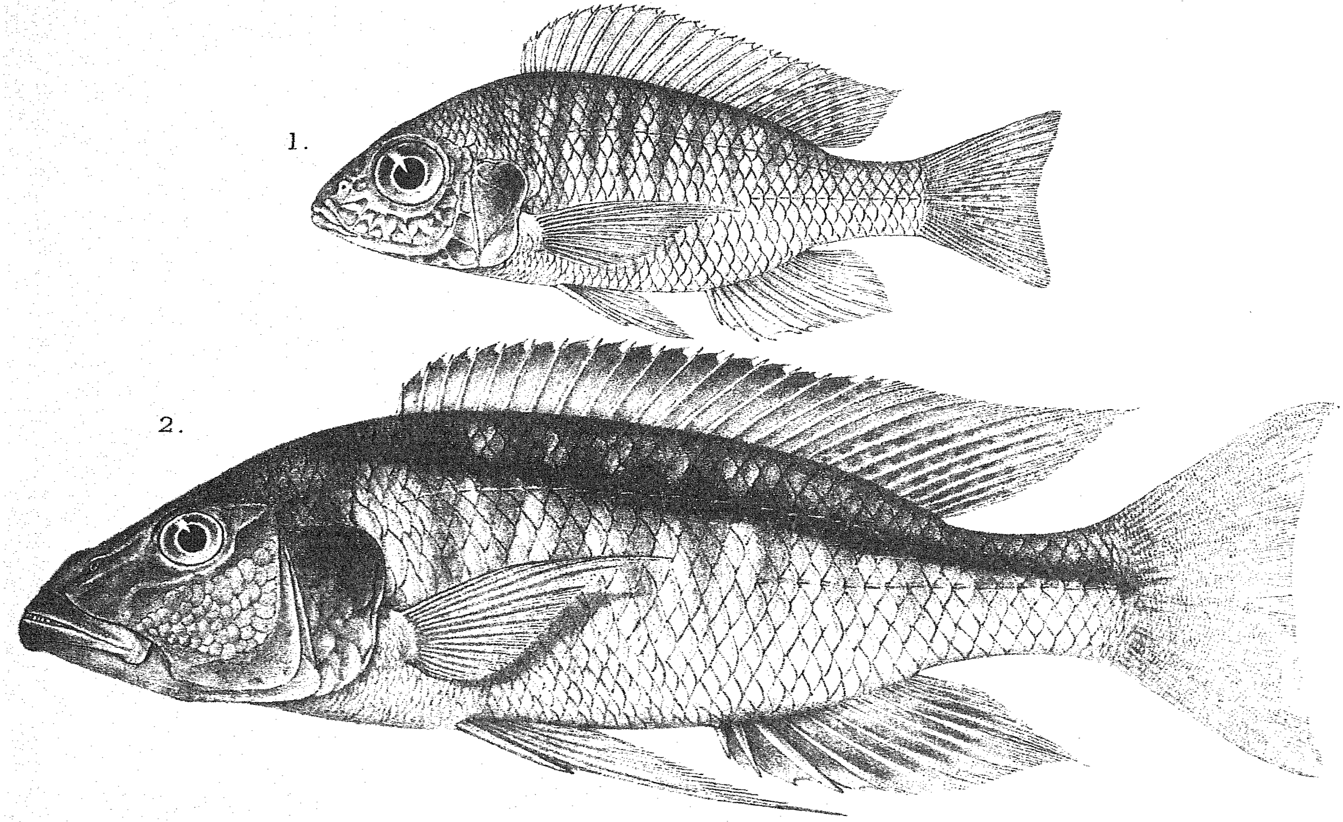
2.



J.Green del. et lith.

Huth imp.

1, HAPLOCHROMIS EUCINOSTOMUS. 2, H. MACROSTOMA, 2/3.

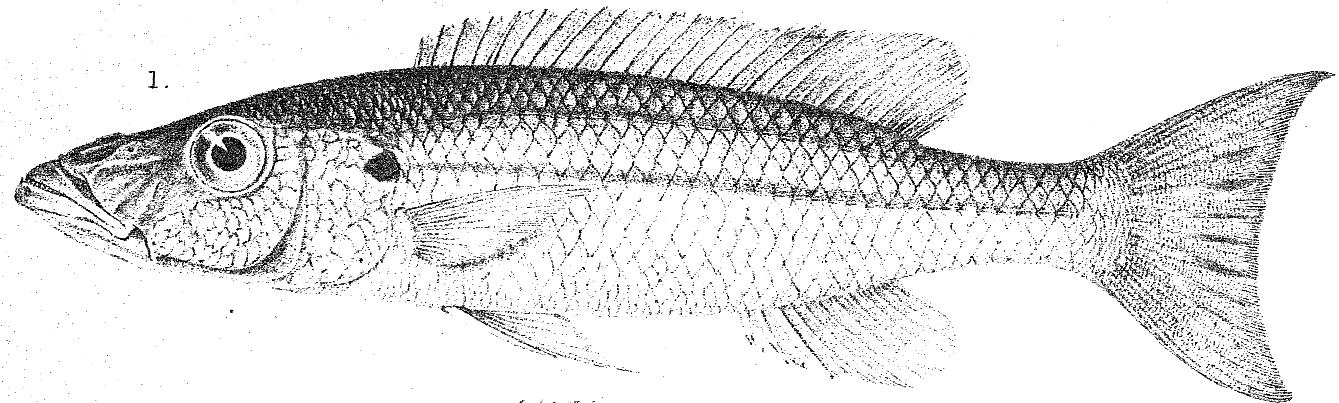


J. Green del. et lith.

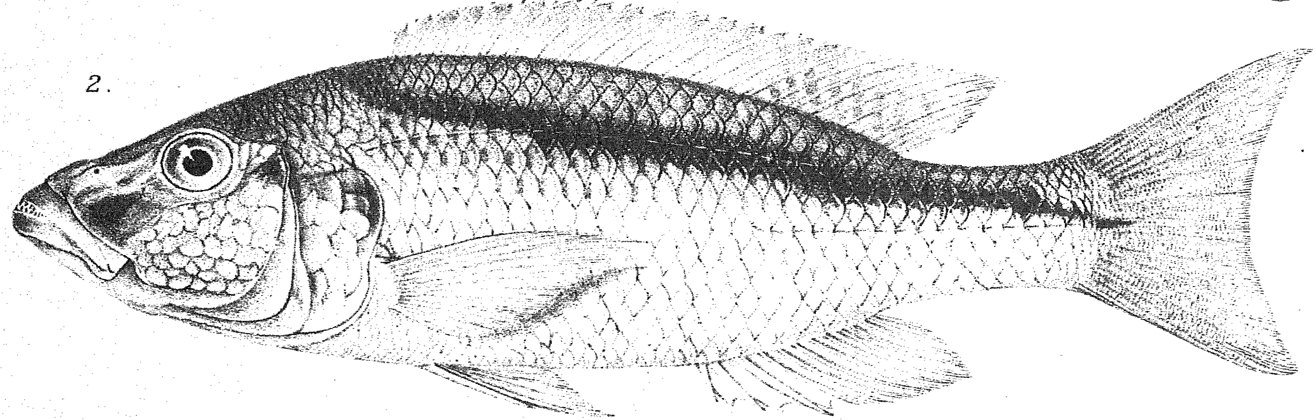
Huth imp.

1, AULONOCARA NYASSÆ, 2, HAPLOCHROMIS LONGIPES. $^{2}/_{3}$.

1.



2.



J. Green del. et lith.

Huth imp.

1, RHAMPHOCHROMIS MACROPHTHALMUS, ¾. 2, HAPLOCHROMIS SPILORHYNCHUS, ¾.

36. The Cichlid Fishes of Lake Nyassa.

By C. TATE REGAN, M.A., F.R.S., F.Z.S., Keeper of Zoology, British Museum (Natural History).

[Received June 7, 1921: Read June 7, 1921.]

(Plates I.–VI.*; Text-figures 1–30.)

The Fishes of Nyassa have been somewhat neglected in comparison with those of Tanganyika and Victoria. They were first described by Günther (P. Z. S. 1864) from specimens collected by Sir John Kirk, and nearly thirty years had passed before the same author again described fishes from the lake sent by Sir Harry Johnston (P. Z. S. 1893). Later a collection made by Captain E. L. Rhoades was described by Boulenger (Ann. & Mag. N. H. (8) ii. 1908). In Boulenger's 'Catalogue of African Fresh-water Fishes,' iii. (1915), 38 species of Cichlidæ are recorded from Nyassa; one of these, *Petrochromis nyassæ*, may now be removed from the list. The supposed occurrence of the specialized Tanganyika genus *Petrochromis* in Nyassa was difficult to explain; re-examination of the type of *P. nyassæ* leads me to regard it as identical with the more recently described *P. fasciolatus*, and I have no doubt that the locality assigned to it was an error on the part of the collector. The loss of this species from the Nyassa list is made good by the re-establishment of Günther's *Chromis subocularis*, placed by Boulenger in the synonymy of *C. johnstoni*, so that the number of valid species of Cichlidæ hitherto described from Nyassa is 38.

The present revision is based on an examination of the specimens in the collection of the British Museum (Natural History), including the types of all the species described by Günther and by Boulenger, but principally on the study of a very fine collection made and presented to the Museum by Mr. Rodney C. Wood. As a result, the number of species is more than doubled, 46 being described below as new to science. Of the 84 species all but 5 (3 *Tilapia*, 1 *Astatotilapia*, 1 *Serranochromis*) are endemic, and the proportion of endemic genera is high, 11 out of 15, but more than half the species belong to the widely distributed genus *Haplochromis*. The majority of the Nyassa genera are quite distinct from any found elsewhere: for example, *Rhamphochromis*, which may be supposed to occupy the same place in Nyassa that *Bathybates* does in Tanganyika, is very different from *Bathybates*. There are, however, a few remarkable examples of convergent evolution in Nyassa and Tanganyika†. The fish described below as *Pseudotropheus tropheops* bears a great superficial resemblance to *Tropheus*, and has the same peculiar dentition; another new type, *Aulonocara*, has deep channels with large openings in the frontal, nasal, orbital, præopercular, and mandibulary bones, exactly as in *Trematocara*.

---

* For explanation of the Plates see p. 727.

† For the Tanganyika genera see Regan, Ann. & Mag. N. H. (9) v. 1920, p. 33.

Synopsis of the Genera.

I. Scales cycloid or very finely denticulate.
  A. Pharyngeal apophysis formed by parasphenoid only.
Teeth in narrow or moderately broad bands, outer bicuspid, inner tricuspid .... 1. *Tilapia.*
Teeth very small, in very broad bands .... 2. *Corematodus.*
Teeth in a few series, slender, with expanded crowns, the outer obliquely truncated .... 3. *Hemitilapia.*
  B. Pharyngeal apophysis formed by parasphenoid in middle and prootics at sides.
Teeth moderate, outer mostly bicuspid, inner tricuspid..... 4. *Otopharynx.*
Teeth very stout, unicuspid.................... 5. *Chilotilapia.*

II. Scales usually distinctly denticulate. Pharyngeal apophysis formed by parasphenoid in middle and basioccipital at sides.
  A. Bones of head with small muciferous canals with small pores.
    1. Præmaxillaries without anterior beak-like expansion.
      a. Edge of membrane of spinous dorsal produced into lappets.
        α. Teeth conical, or outer bicuspid and inner tricuspid.
Teeth of outer series in upper jaw first decreasing and then increasing in size antero-posteriorly; band of teeth in lower jaw crescentic .... 6. *Astatotilapia.*
Upper jaw with a rather broad band of small cuspidate teeth anteriorly and a series of enlarged conical teeth on each side; lower jaw with a band of teeth with incurved lateral edges, from which a single series runs back on each side .... 7. *Pseudotropheus.*
Teeth conical; lower jaw with 4 anterior canines .... 8. *Cynotilapia.*
Teeth conical; no canines; 7 to 9 series of scales on cheek. 9. *Serranochromis.*
Outer teeth decreasing in size posteriorly; no distinct canines; bands of teeth continuous; 2 to 6 series of scales on cheek .... 10. *Haplochromis.*
Teeth very small and slender, forming narrow bands which are interrupted at the symphyses .... 11. *Lethrinops.*
        β. Outer teeth very broad, compressed, with or without a pair of small lateral cusps .... 12. *Docimodus.*
      b. Edge of membrane of spinous dorsal running evenly between the tips of the spines .... 13. *Cyrtocara.*
    2. Præmaxillaries with an anterior beak-like expansion.
14. *Rhamphochromis.*
  B. Frontals, nasals, orbitals, præopercular and mandibulary bones deeply excavated, with large openings .... 15. *Aulonocara.*

1. Tilapia A. Smith, 1840
(type *T. sparmanni* A. Smith).

Teeth small or moderate, in several series, the outer bicuspid, the inner tricuspid (sometimes conical in large fish). Scales cycloid or feebly denticulate. Pharyngeal apophysis formed by parasphenoid only.

Africa; numerous species.

The four species found in Nyassa may be distinguished as follows:—

I. Three anal spines.
  A. Caudal scaled only at the base.
Maxillary extending to below eye .... 1. *massambica.*
Maxillary not extending to below eye .... 2. *melanopleura.*
  B. Caudal covered with small scales .... 3. *squamipinnis.*
II. Four anal spines .... 4. *shirana.*

1. Tilapia mossambica Peters, 1852.

Bouleng. Cat. Afr. Fish. iii. p. 154, fig. 101.
East Africa.

2. Tilapia melanopleura A. Dum., 1859.

Bouleng. Cat. Afr. Fish. iii. p. 190, fig. 123.
West Africa, Congo, and Zambesi.

3. Tilapia squamipinnis Günth., 1864.

Bouleng. Cat. Afr. Fish. iii. p. 183, fig. 118.
Nyassa.

4. Tilapia shirana Bouleng., 1896.

Bouleng. Cat. Afr. Fish. iii. p. 151, fig. 98.
Nyassa and Portuguese E. Africa.

2. Corematodus Bouleng., 1896.

Jaws with very broad bands of very small teeth, the outer with expanded, compressed, and obliquely truncated crowns, the inner mostly pointed. Scales cycloid.

A single species from Nyassa.

Corematodus shiranus Bouleng., 1896.

Corematodus shiranus Bouleng. Cat. Afr. Fish. iii. p. 494, fig. 342.

Depth of body 2⅔ in length, length of head 3. Snout with convex profile, shorter than postorbital part of head. Diameter of eye equal to praeorbital depth, 5 in length of head; interorbital width 2⅔. Jaws equal anteriorly; maxillary extending to below eye. 4 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 34 scales in a longitudinal series. Dorsal XVI 11; last spine ⅔ length of head. Anal III 9; third spine ⅓ length of head. Caudal scaly. Caudal peduncle 1½ as long as deep. Body with seven narrow blackish cross-bars as in *Tilapia squamipinnis*, the first downwards from origin of dorsal, the last two on caudal peduncle.

The type, 200 mm. long.

3. Hemitilapia Bouleng., 1902.

Teeth in 3 to 6 series, small, with slender shaft and compressed and expanded crown, those of outer series obliquely truncated. Scales feebly denticulate.

A single species from Nyassa.

Hemitilapia oxyrhynchus Bouleng., 1902.

Hemitilapia oxyrhynchus Bouleng. Cat. Afr. Fish. iii. p. 489, fig. 339.

Depth of body $2\frac{2}{5}$ to $2\frac{2}{3}$ in the length, length of head 3 to $3\frac{1}{3}$. Snout with straight or concave profile, from as long as to $1\frac{3}{4}$ diameter of eye, which is $3\frac{1}{4}$ to $5\frac{1}{2}$ in length of head, in adult equal to præorbital depth; interorbital width $3\frac{1}{2}$ to 4 in head. Jaws equal; maxillary not extending to below eye. 3 or 4 series of scales on cheek. 12 or 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 to 35 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI 10–11; last spine from less than $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 9–10; third spine from less than $\frac{1}{3}$ to more than $\frac{2}{5}$ head. Pectoral as long as or a little shorter than head. Caudal scaly, truncate or slightly emarginate. Caudal peduncle longer than deep. A dark spot on operculum, usually two on lateral line below spinous and soft dorsal respectively and another at base of caudal. Dorsal and caudal spotted with orange; anal with long spots between the rays; males with dorsal, anal, and pelvic fins darker, pale-edged.

Seven specimens, 90 to 190 mm. long. (*Moore*, *Rhoades*, *Wood*).

4. OTOPHARYNX Regan, 1920
(type *Tilapia auromarginata* Bouleng.).

As *Tilapia*, but the prootic forms part of the facet for articulation of the upper pharyngeal on each side.

Nyassa; two species.

1. OTOPHARYNX AUROMARGINATUS Bouleng., 1908.

Tilapia auromarginata Bouleng. Cat. Afr. Fish. iii. p. 180, fig. 115.

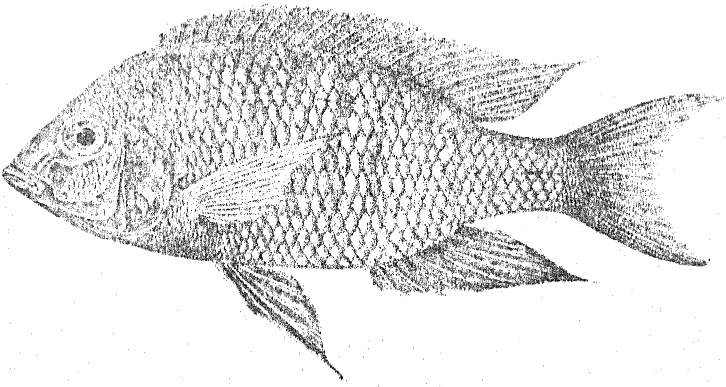
Depth of body $2\frac{1}{2}$ to $2\frac{2}{3}$ in length, length of head $3\frac{1}{3}$ to $3\frac{1}{2}$. Snout decurved, as long as or a little shorter than postorbital part of head. Diameter of eye equal to depth of præorbital, $3\frac{3}{4}$ to 4 in length of head; interorbital width 3 to $3\frac{1}{3}$. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 3 to 5 series, inner tricuspid or conical; 60 to 75 in outer series of upper jaw, the anterior bicuspid, the posterior conical. 4 series of scales on cheek. 15 to 18 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. Scales cycloid, 33 or 34 in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVII–XVIII 10–11; last spine $\frac{2}{5}$ length of head or a little more. Anal III 9–10; third spine stronger than dorsals, $\frac{1}{3}$ head or a little more. Pectoral as long as head, not reaching anal. Caudal densely scaled, emarginate. Caudal peduncle $1\frac{1}{4}$ as long as deep. Bluish; dorsal and anal dark blue with yellow edge; dorsal with series of red spots.

Two specimens, 205 and 240 mm. in length, and a skeleton.

2. Otopharynx selenurus, sp. n. (Text-fig. 1.)

Depth of body 2½ in length, length of head 3⅓. Snout with straight profile, as long as postorbital part of head. Diameter of eye nearly equal to depth of præorbital or cheek, 4 to 4½ in length of head, interorbital width 4. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 3 or 4 series, 50 to 55 bicuspid teeth in outer series of upper jaw. 3 or 4 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. 35 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI XVII 11–12; last spine ⅔ length of head, longest soft rays nearly as long as head. Anal III 9; third spine stronger and shorter than last dorsal. Pectoral as long as head, reaching anal. Caudal scaly, deeply emarginate. Caudal peduncle 1½ as long as deep. Bluish grey, uniform or with traces of darker cross-bars.

Text-figure 1.



Otopharynx selenurus. ½.

Two specimens, 135 and 155 mm. in total length (*Wood*).

A smaller example, 90 mm. long, is more slender (depth 3 in length), but, except for juvenile characters, such as the larger eye (3¼ in head), is very similar to the two described; colour silvery, with traces of several cross-bars; an oblong dark spot on lateral line below middle of spinous dorsal, a band along lower lateral line.

5. Chilotilapia Bouleng., 1908.

Jaws with an outer series of stout, little compressed, teeth, and 3 or 4 inner series of smaller subconical teeth, which are stronger at the sides of the præmaxillaries than in front. Scales cycloid or feebly denticulate.

Nyassa; a single species.

CHILOTILAPIA RHOADESII Bouleng., 1908.

Chilotilapia rhoadesii Bouleng. Cat. Afr. Fish. iii. p. 499, fig. 366.

Depth of body $2\frac{1}{3}$ to $2\frac{1}{2}$ in the length, length of head $3\frac{1}{2}$. Snout short, declivous; diameter of eye 4 to $4\frac{1}{2}$ in length of head, præorbital depth 4, interorbital width 3. Jaws equal anteriorly; mouth wide, with short lateral cleft. 3 or 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth moderately strong, subconical. 32 to 34 scales in a longitudinal series. Dorsal XV–XVI 10; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 9–10. Pectoral a little longer than head, reaching anal. Caudal densely scaled, emarginate. Caudal peduncle a little longer than deep. Silvery or bluish; an opercular spot; sometimes a broad dark band on each side of back and another on middle of side; soft dorsal with series of spots.

The type (220 mm.) and two specimens of 180 and 200 mm. (*Wood*).

6. ASTATOTILAPIA Pellegr., 1904
(type *Labrus desfontainesii* Lacep.).

Near *Haplochromis*, but posterior teeth of outer series of upper jaw increasing in size backwards. Teeth in 3 to 5 series, cuspidate or conical, those of outer series of upper jaw sometimes bicuspid anteriorly, conical posteriorly; band of teeth in lower jaw crescentic. Middle teeth of lower pharyngeal somewhat enlarged. Dorsal XIII–XVII 8–11. Anal III 7–11. Scales 26 to 36.

Africa.

This genus includes three species placed by Boulenger in *Tilapia*, namely, *T. swynnertoni*, *T. burtoni*, and *T. calliptera*, and four included by him in *Haplochromis*, *H. strigigena*, *H. moffati*, *H. desfontainesii*, and *H. moeruensis*. These are all closely related, agreeing in the form and size of the mouth, the rather short pectorals, comparatively short caudal peduncle (as long as deep), and the rounded caudal.

ASTATOTILAPIA CALLIPTERA Günth., 1893.

Tilapia calliptera Bouleng. Cat. Afr. Fish. iii. p. 222, fig. 145.

Depth of body $2\frac{1}{2}$ to $2\frac{4}{5}$ in length, length of head $2\frac{3}{4}$ to $3\frac{1}{5}$. Snout with straight profile, shorter than postorbital part of head. Diameter of eye $3\frac{1}{2}$ to $4\frac{1}{2}$ in length of head, in adult scarcely greater than depth of præorbital; interorbital width $3\frac{1}{2}$ to $4\frac{1}{3}$ in length of head. Jaws equal anteriorly; maxillary extending to below anterior edge of eye; teeth in 3 to 5 series, 40 to 60 in outer series of upper jaw, the anterior bicuspid, the last 2 or 3 (young) or 8 or 9 (adult), conical, increasing in size posteriorly. 3 to 5 series of scales on cheek. 8 to 10 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth rather strong, conical in adult. 29 to 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XIV–XVI 8–11; last spine ⅖ to ½ length of head. Anal III 7–9; third spine stronger and usually shorter than last dorsal. Pectoral shorter than head, not reaching anal. Caudal rounded. Caudal peduncle as long as deep. An opercular spot and a dark bar from eye to end of maxillary; body with or without dark cross-bars and a dark lateral band; dorsal and caudal sometimes spotted; males with lower fins blackish, the anal with 2 to 6 rounded orange spots.

Nyassa and Zambezi.

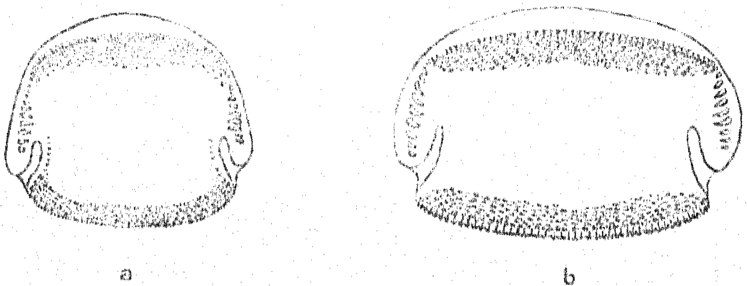
Numerous specimens, 65 to 140 mm. in total length.

7. Pseudotropheus, gen. n.
(type *Chromis williamsi* Günth.).

Jaws with several series of teeth anteriorly, the outer bicuspid, the inner small and tricuspid, forming rather broad curved or transverse bands; upper jaw with a series of conical teeth on each side posteriorly, more or less sharply differentiated, some or all larger than the last bicuspid teeth; lower jaw short and broad, with the lateral margin of the band of teeth incurved, and with a series of teeth on each side behind the band. Dorsal XVI–XIX 8–10. Anal III 7–9. Scales denticulate.

Nyassa; five species.

Text-figure 2.



a. Dentition of *Pseudotropheus tropheops*.
b. „ *Tropheus moorii*.

Synopsis of Species.

I. Jaws equal anteriorly.
D. XVI–XVII 9. A. III 8. 4 series of scales on cheek .... 1. *williamsi*.
D. XVIII 9. A. III 9. 5 or 6 series of scales on cheek .... 2. *zebra*.

II. Lower jaw shorter than upper; mouth rounded.
D. XVIII 9. A. III 8. Depth 3 in length .... 3. *novemfasciatus*.
D. XIX 8. A. III 7. Depth 3⅔ in length .... 4. *auratus*.

III. Mouth subterminal, transverse; snout very convex.
D. XVII 10. A. III 8 .... 5. *tropheops*.

1. PSEUDOTROPHEUS WILLIAMSI Günth., 1893.

Chromis williamsi Günth. P. Z. S. 1893, p. 624, pl. lvi. fig. C.

Tilapia livingstonii Bouleng. P. Z. S. 1899, p. 134, pl. x. fig. 2; Cat. Afr. Fish. iii. p. 243, fig. 162.

Tilapia williamsi Bouleng. Cat. Afr. Fish. iii. p. 225, fig. 147.

Depth of body equal to length of head, 3 in length of fish. Upper profile of head convex; snout as long as or a little longer than diameter of eye, which is 3½ to 4 in length of head, nearly equal to or greater than the interorbital width, depth of cheek, or præorbital. Mouth terminal, rounded; maxillary extending to below anterior edge of eye; teeth in 5 or 6 series, inner small, tricuspid: 49 to 52 teeth in outer series of upper jaw, the last 3 or 4 (young) or 6 to 9 (adult) on each side conical, enlarged and sharply differentiated from the rest, which are bicuspid. 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender. 33 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI–XVII 9; last spine a little less than ½ length of head. Anal III 8; third spine a little shorter than dorsal. Pectoral ¾ length of head, not reaching anal. Caudal truncate ?, densely scaled in basal half. Caudal peduncle as long as or a little longer than deep. Body with 6 dark cross-bars, or bars represented by a series of spots above lateral line and another on middle of side; an opercular spot and a dark bar or spot on base of caudal; two round white (? orange) spots on anal fin (probably absent in ♀).

Two specimens, types of the species and of *T. livingstonii*, 105 and 75 mm. long.

2. PSEUDOTROPHEUS ZEBRA Bouleng., 1899.

Tilapia zebra Bouleng. Cat. Afr. Fish. iii. p. 244, fig. 163 (1915).

Depth of body 2½ in length, length of head 3⅕. Snout decurved, a little longer than diameter of eye, which is 4 in length of head, a little greater than depth of præorbital, equal to depth of cheek; interorbital width 3 in length of head. Mouth terminal, rounded, rather wide; jaws equal anteriorly; maxillary extending to vertical from anterior edge of eye; teeth in 4 or 5 series, 56 in outer series of upper jaw, the last 8 or 9 conical. 5 or 6 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. 31 scales in a longitudinal series, 8 from origin of dorsal to lateral line. Dorsal XVIII 9; last spine nearly ½ length of head. Anal III 9; third spine a little shorter than last dorsal. Pectoral nearly as long as head, not reaching anal. Caudal probably truncate, densely scaled at base. Caudal peduncle a little deeper than long. A dark bar between eyes, a second from opercular spot to occiput; 6 vertical bars on body, the first from origin of dorsal to base of pectoral, the sixth from soft dorsal to anal; three round pale (? orange) spots on anal in male.

The type, 105 mm. in total length.

3. Pseudotropheus novemfasciatus, sp. n.

Depth of body 3 in length, length of head 3¼. Snout with convex profile, as long as diameter of eye, which is 3½ in length of head, equal to interorbital width, greater than depth of præorbital or cheek. Mouth rounded, lower jaw shorter than upper; maxillary reaching vertical from anterior edge of eye; teeth in 5 or 6 series, about 40 in outer series of upper jaw, anteriorly bicuspid, the last 6 to 8 on each side conical, some enlarged. 5 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVIII 9; last spine ½ length of head. Anal III 8; third spine as long as and stronger than last dorsal. Pectoral shorter than head, not reaching anal. Caudal truncate. Caudal peduncle as long as deep. Body crossed by 9 dark vertical bars, the first 6 corresponding to the 6 of *P. zebra*, the last 2 on caudal peduncle; end of snout and lower jaw blackish; an opercular spot and a spot on base of caudal; a faint dark band on lateral line and another on middle of side; spinous dorsal with a dusky intramarginal band; soft dorsal and caudal with series of spots.

A single specimen, 65 mm. in total length (*Wood*).

4. Pseudotropheus auratus Bouleng., 1897.

Tilapia aurata Bouleng. Cat. Afr. Fish. iii. p. 246, fig. 164.

Depth of body 3⅔ in length, length of head 3⅓. Snout with convex profile, a little longer than diameter of eye, which is 4 in length of head, a little greater than interorbital width, depth of præorbital, or cheek. Mouth rounded; lower jaw shorter than upper; maxillary nearly reaching vertical from anterior edge of eye; teeth in 5 or 6 series, 45 in outer series of upper jaw, the last 4 or 5 conical, enlarged. 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. 33 scales in a longitudinal series. Dorsal XIX 8; last spine ⅖ length of head. Anal III 7; third spine as long as last dorsal. Pectoral ¾ length of head, not reaching anal. Caudal densely scaled, truncate. Caudal peduncle a little longer than deep. Lips blackish; two black bands between eyes; a black stripe from eye, ending in a spot on base of caudal; a second near edge of back, a third on dorsal fin.

The type, 75 mm. in total length.

5. Pseudotropheus tropheops, sp. n. (Text-fig. 3.)

Depth of body 2⅔ to 3 in length, length of head 3½. Upper profile of head very convex; snout as long as diameter of eye, which is 3⅔ in length of head, slightly exceeds præorbital depth and equals depth of cheek; interorbital region convex, its width 2⅔ to 2¾ in length of head. Mouth subterminal, transverse; jaws with 8 series of small cuspidate teeth; a series of 6 to 8 well-differentiated conical teeth on each side of præmaxillary. 4 series of scales on

1. Pseudotropheus williamsi Günth., 1893.

Chromis williamsi Günth. P. Z. S. 1893, p. 624, pl. lvi. fig. C.

Tilapia livingstonii Bouleng. P. Z. S. 1899, p. 134, pl. x. fig. 2; Cat. Afr. Fish. iii. p. 243, fig. 162.

Tilapia williamsi Bouleng. Cat. Afr. Fish. iii. p. 225, fig. 147.

Depth of body equal to length of head, 3 in length of fish. Upper profile of head convex; snout as long as or a little longer than diameter of eye, which is 3½ to 4 in length of head, nearly equal to or greater than the interorbital width, depth of cheek, or præorbital. Mouth terminal, rounded; maxillary extending to below anterior edge of eye; teeth in 5 or 6 series, inner small, tricuspid: 40 to 52 teeth in outer series of upper jaw, the last 3 or 4 (young) or 6 to 9 (adult) on each side conical, enlarged and sharply differentiated from the rest, which are bicuspid. 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender. 33 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI-XVII 9; last spine a little less than ½ length of head. Anal III 8; third spine a little shorter than dorsal. Pectoral ¾ length of head, not reaching anal. Caudal truncate ?, densely scaled in basal half. Caudal peduncle as long as or a little longer than deep. Body with 6 dark cross-bars, or bars represented by a series of spots above lateral line and another on middle of side; an opercular spot and a dark bar or spot on base of caudal; two round white (? orange) spots on anal fin (probably absent in ♀).

Two specimens, types of the species and of *T. livingstonii*, 105 and 75 mm. long.

2. Pseudotropheus zebra Bouleng., 1899.

Tilapia zebra Bouleng. Cat. Afr. Fish. iii. p. 244, fig. 163 (1915).

Depth of body 2½ in length, length of head 3⅕. Snout decurved, a little longer than diameter of eye, which is 4 in length of head, a little greater than depth of præorbital, equal to depth of cheek; interorbital width 3 in length of head. Mouth terminal, rounded, rather wide; jaws equal anteriorly: maxillary extending to vertical from anterior edge of eye; teeth in 4 or 5 series, 56 in outer series of upper jaw, the last 8 or 9 conical. 5 or 6 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. 31 scales in a longitudinal series, 8 from origin of dorsal to lateral line. Dorsal XVIII 9; last spine nearly ½ length of head. Anal III 9; third spine a little shorter than last dorsal. Pectoral nearly as long as head, not reaching anal. Caudal probably truncate, densely scaled at base. Caudal peduncle a little deeper than long. A dark bar between eyes, a second from opercular spot to occiput; 6 vertical bars on body, the first from origin of dorsal to base of pectoral, the sixth from soft dorsal to anal; three round pale (? orange) spots on anal in male.

The type, 105 mm. in total length.

3. Pseudotropheus novemfasciatus, sp. n.

Depth of body 3 in length, length of head $3\frac{1}{4}$. Snout with convex profile, as long as diameter of eye, which is $3\frac{1}{2}$ in length of head, equal to interorbital width, greater than depth of præorbital or cheek. Mouth rounded, lower jaw shorter than upper; maxillary reaching vertical from anterior edge of eye; teeth in 5 or 6 series, about 40 in outer series of upper jaw, anteriorly bicuspid, the last 6 to 8 on each side conical, some enlarged. 5 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVIII 9; last spine $\frac{1}{2}$ length of head. Anal III 8; third spine as long as and stronger than last dorsal. Pectoral shorter than head, not reaching anal. Caudal truncate. Caudal peduncle as long as deep. Body crossed by 9 dark vertical bars, the first 6 corresponding to the 6 of *P. zebra*, the last 2 on caudal peduncle; end of snout and lower jaw blackish; an opercular spot and a spot on base of caudal; a faint dark band on lateral line and another on middle of side; spinous dorsal with a dusky intramarginal band; soft dorsal and caudal with series of spots.

A single specimen, 65 mm. in total length (*Wood*).

4. Pseudotropheus auratus Bouleng., 1897.

Tilapia aurata Bouleng. Cat. Afr. Fish. iii. p. 246, fig. 164.

Depth of body $3\frac{2}{3}$ in length, length of head $3\frac{1}{3}$. Snout with convex profile, a little longer than diameter of eye, which is 4 in length of head, a little greater than interorbital width, depth of præorbital, or cheek. Mouth rounded; lower jaw shorter than upper; maxillary nearly reaching vertical from anterior edge of eye; teeth in 5 or 6 series, 45 in outer series of upper jaw, the last 4 or 5 conical, enlarged. 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. 33 scales in a longitudinal series. Dorsal XIX 8; last spine $\frac{2}{5}$ length of head. Anal III 7; third spine as long as last dorsal. Pectoral $\frac{3}{4}$ length of head, not reaching anal. Caudal densely scaled, truncate. Caudal peduncle a little longer than deep. Lips blackish; two black bands between eyes; a black stripe from eye, ending in a spot on base of caudal; a second near edge of back, a third on dorsal fin.

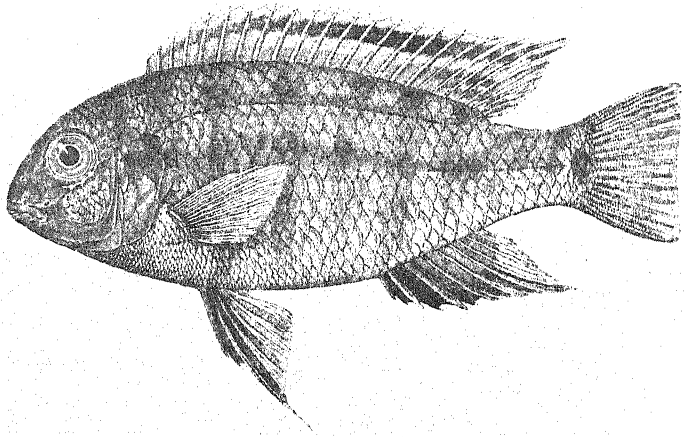
The type, 75 mm. in total length.

5. Pseudotropheus tropheops, sp. n. (Text-fig. 3.)

Depth of body $2\frac{2}{3}$ to 3 in length, length of head $3\frac{1}{2}$. Upper profile of head very convex; snout as long as diameter of eye, which is $3\frac{2}{3}$ in length of head, slightly exceeds præorbital depth and equals depth of cheek; interorbital region convex, its width $2\frac{2}{3}$ to $2\frac{3}{4}$ in length of head. Mouth subterminal, transverse; jaws with 8 series of small cuspidate teeth; a series of 6 to 8 well-differentiated conical teeth on each side of præmaxillary. 4 series of scales on cheek. 9 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender. 33 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVII 10; last spine $\frac{1}{2}$ length of head. Anal III 8; third spine stronger and as long as or a little shorter than last dorsal. Pectoral a little shorter than head, not reaching anal. Caudal scaly, truncate. Caudal peduncle as long as or a little longer than deep. Traces of dark cross-bars on body bearing a series of darker spots above lateral line and another on middle of side; an opercular spot and a spot on base of caudal; dorsal with a blackish intramarginal band.

Two specimens, 116 and 122 mm. in total length (*Wood*).

Text-figure 3.



Pseudotropheus tropheops. $\frac{1}{1}$.

8. Cynotilapia, gen. n.

Near *Pseudotropheus*, but teeth conical, in a few series, outer large, in lower jaw forming distinct canines anteriorly.

Nyassa; a single species.

Cynotilapia afra Günth., 1893.

Paratilapia afra Bouleng. Cat. Afr. Fish. iii. p. 325, fig. 218.

Depth of body $2\frac{3}{4}$ to 3 in length, length of head 3 to $3\frac{1}{4}$. Snout decurved, as long as or a little longer than diameter of eye, which is $3\frac{1}{3}$ to $3\frac{1}{2}$ in length of head, greater than præorbital depth; interorbital width $3\frac{1}{3}$ in length of head. Jaws equal anteriorly; maxillary not quite reaching vertical from anterior edge of eye; teeth conical, triserial, outer large, 28 to 32 in upper jaw; lower jaw with four strong anterior canines. 3 or 4 series of scales in cheek. 14 or 15 gill-rakers on lower part of anterior arch. 33 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVII 9; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 8; third spine stronger and as long as or a little shorter than last dorsal. Pectoral shorter than head, not reaching anal. Caudal? Caudal peduncle as long as or longer than deep.

The types, 85 and 95 mm. in total length.

9. SERRANOCHROMIS Regan, 1920.

As *Haplochromis*, but third vertebra without inferior apophyses, fourth with a very small pair. Mouth large; teeth conical; cheek deep, with 7 to 9 series of scales.

A single species.

SERRANOCHROMIS THUMBERGII Casteln., 1861.

Paratilapia thumbergii Bouleng. Cat. Afr. Fish. iii. p. 328, fig. 220.

Nyassa and Zambezi; Katanga and L. Bangwelu; L. Ngami; Angola.

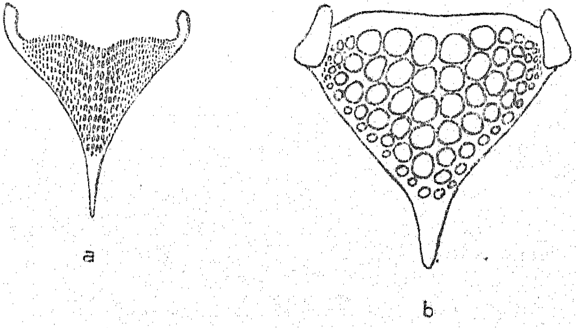
10. HAPLOCHROMIS Hilgend., 1888
(type *H. obliquidens* Hilgend.).

Ctenochromis Pfeff., 1893 (*pectoralis*).

Champsochromis Bouleng., 1915 (*cœruleus*).

An outer series of bicuspid or conical teeth, decreasing in size posteriorly, and one or more inner series of smaller bicuspid or conical teeth. 2 to 6 series of scales on cheek. Scales usually distinctly denticulate. Pharyngeal apophysis formed by parasphenoid in middle and basioccipital at sides. Third vertebra with inferior apophyses, which meet below.

Text-figure 4.



a. Lower pharyngeal of *Haplochromis tetrastigma*.
b. „ „ *H. placodon*.

52 species of this genus occur in Nyassa, all of them endemic. In the great number and diversity of species of *Haplochromis*

Nyassa resembles Victoria and differs notably from Tanganyika. In the Nyassa species the caudal fin is truncate or emarginate, and appears to be always nearly completely covered with small scales in the adult fish; this feature, the prevalence of a few distinctive types of coloration, and the absence of evident relationship to species found elsewhere lead to the conclusion that the Nyassa species are a natural group and may perhaps have evolved in the lake from a single ancestral form. This conclusion is fortified by the study of such skeletons as are available.

The differences in the pharyngeal dentition between closely related species are sometimes very striking; the best examples of this are *H. tetrastigma* and *H. placodon*, and *H. similis* and *H. kirkii*; these cases make it evident that it is not desirable to regard the development of large, round, blunt pharyngeal teeth as warranting generic separation.

Synopsis of the Nyassa Species.

I. Snout not longer than postorbital part of head.

A. Pectoral fin with series of spots on the rays.

Lower jaw projecting .... 1. *livingstonii.*

Jaws equal; depth of body 2⅗ to 3 in length .... 2. *polystigma.*

Jaws equal; depth 2⅖ in length .... 3. *maculimanus.*

B. Pectoral fin immaculate.

1. Præmaxillary pedicels not extending beyond anterior edge of orbits.

a. Body with a series of dark spots on back alternating with a series on or above middle of side, or uniting with them to form irregular cross-bars. Jaws equal; outer teeth mostly bicuspid.

Pharyngeal teeth small; spots very large .... 4. *simulans.*

Middle pharyngeal teeth enlarged, blunt; caudal peduncle 1½ to 1¾ as long as deep .... 5. *subocularis.*

Middle pharyngeal teeth enlarged, blunt; caudal peduncle a little longer than deep .... 6. *ornatus.*

b. Body with 6 dark cross-bars. Lower jaw projecting; outer teeth bicuspid.

Pharyngeal teeth small .... 7. *johnstoni.*

Lower pharyngeal with a group of enlarged blunt teeth ... 8. *sexfasciatus.*

c. Body with a dark lateral stripe, slightly curved anteriorly, from head to caudal fin. Outer teeth bicuspid.

α. Lower jaw a little projecting; middle pharyngeal teeth stout and blunt .... 9. *kirkii.*

β. Jaws equal; pharyngeal teeth small.

Caudal truncate or slightly emarginate .... 10. *similis.*

Caudal rather deeply emarginate; 45 to 60 teeth in outer series .... 11. *breviceps.*

Caudal rather deeply emarginate; 24 to 30 teeth in outer series .... 12. *microstoma.*

d. Body with a dark lateral band on tail, continued forward as a series of spots. Teeth conical. Lower jaw projecting. 13. *urotænia.*

e. Body with a straight dark band or stripe from head to caudal fin. Teeth conical. Lower jaw projecting.

α. Mouth little oblique, below level of eye.

Caudal truncate or very slightly emarginate .... 14. *fuscotæniatus.*

Caudal distinctly emarginate .... 15. *holotænia.*

β. Mouth very oblique, anteriorly on a level with eye.

Depth of body 2⅔ to 2⅘ in length .... 16. *strigatus.*

Depth of body 4 in length .... 17. *dimidiatus.*

f. An opercular spot and a blackish spot on or under lateral line below middle of spinous dorsal; often a third spot below soft dorsal and a fourth at base of caudal ‡.

α. 8 to 13 gill-rakers on lower part of anterior arch (? *H. intermedius*).

* Outer teeth bicuspid; lower jaw not projecting.

Maxillary extending to below eye .... 18. *auritus*.
Maxillary not extending to below eye; pharyngeal teeth small .... 19. *tetrastigma*.
Maxillary not extending to below eye; pharyngeal teeth large, rounded, blunt .... 20. *placodon*.

** Outer teeth conical; lower jaw projecting (? *H. intermedius*).

Snout a little shorter than postorbital part of head; last dorsal spine nearly $\frac{1}{2}$ length of head .... 21. *intermedius*.
Snout as long as postorbital part of head; last dorsal spine $\frac{1}{3}$, interorbital width $\frac{1}{5}$ length of head .... 22. *modestus*.
Snout as long as postorbital part of head; last dorsal spine $\frac{1}{3}$ to $\frac{2}{5}$, interorbital width $\frac{1}{6}$ or $\frac{1}{7}$ length of head .... 23. *woodi*.

β. 17 to 28 gill-rakers on lower part of anterior arch.

17 to 21 gill-rakers; 15 or 16 dorsal spines .... 24. *chrysonotus*.
23 to 28 gill-rakers; 17 or 18 dorsal spines .... 25. *quadrimaculatus*.

g. A dark band from nape or origin of dorsal to base of caudal (sometimes faint or absent in large specimens).

α. Lower pharyngeal with a group of large, rounded, blunt teeth.

Jaws equal; caudal peduncle $1\frac{1}{4}$ to $1\frac{1}{2}$ as long as deep .... 26. *sphærodon*.
Jaws equal; candal peduncle $1\frac{2}{3}$ as long as deep .... 27. *ericotænia*.
Lower jaw projecting .... 28. *lateristriga*.

β. Lower pharyngeal teeth of the 2 middle series a little enlarged.

Eye 3 to 4 in head (in specimens of 70 to 110 mm.) .... 29. *plagiotænia*.
Eye 3 to $3\frac{1}{2}$ in head (in specimens of 120 to 170 mm.) ... 30. *melanotænia*.

γ. Pharyngeal teeth small; outer teeth of jaws forming a close-set series, usually bicuspid in young, some or all conical in adult.

* Lower jaw a little shorter than upper ... 31. *guentheri*.
** Jaws equal; 18 or 19 dorsal spines ...... 32. *melanonotus*.
*** Jaws equal or lower a little projecting; 15 to 17 dorsal spines.

† Maxillary extending to vertical from anterior edge of eye.

8 or 9 gill-rakers on lower part of anterier arch .... 33. *brevis*.
12 gill-rakers; 35 or 36 scales; caudal peduncle $1\frac{1}{2}$ as long as deep .... 34. *nototænia*.
11 to 13 gill-rakers; 37 to 39 scales; caudal peduncle $1\frac{2}{3}$ to 2 as long as deep .... 35. *lepturus*.

†† Maxillary not extending to below eye.

Scales 35 to 37; last dorsal spine $\frac{1}{4}$ to $\frac{1}{3}$ head .... 36. *rhoadesii*.
Scales 33 or 34; last dorsal spine quite $\frac{2}{5}$ head .... 37. *atritæniatus*.

δ. Pharyngeal teeth slender; outer teeth of jaws conical, rather strong, and spaced.

* Third anal spine as long as last dorsal; pelvic fins shorter than head .... 38. *spilorhynchus*.

** Third anal spine shorter than last dorsal; pelvic fins as long as head.

Maxillary not quite reaching vertical from anterior edge of eye .... 39. *longipes*.
Maxillary not nearly reaching vertical from anterior edge of eye .... 40. *cæruleus*.

h. Coloration silvery, sometimes with faint dark cross-bars.

α. Maxillary extending to below anterior edge of eye.

Lower pharyngeal with a group of enlarged teeth with spherical crowns .... 41. *macrochir*.
Posterior teeth of 2 middle series of lower pharyngeal somewhat enlarged .... 42. *argyrosoma*.

---

‡ I include *H. modestus* here, but its coloration is unknown; the type, as preserved, is uniformly brownish.

β. Maxillary not extending to below eye.

Lower jaw a little the shorter; 12 or 13 gill-rakers on lower part of anterior arch .... 43. *macrophthalmus.*
Jaws equal anteriorly; 11 gill-rakers on lower part of anterior arch .... 44. *leuciscus.*
Jaws equal; 15 or 16 gill-rakers .... 45. *inornatus.*
Lower jaw a little the shorter; 16 or 17 gill-rakers .... 46. *micrentodon.*

2. Præmaxillary pedicels extending to between middle of orbits.
47. *eucinostomus.*

II. Snout longer than postorbital part of head.

A. Lower jaw projecting; maxillary not extending to below eye.

Teeth cuspidate; caudal emarginate .... 48. *præorbitalis.*
Teeth conical; caudal truncate .... 49. *compressiceps.*

B. Jaws equal anteriorly; maxillary not extending to below eye.

15 to 17 gill-rakers on lower part of anterior arch .... 50. *macrorhynchus.*
19 or 20 gill-rakers on lower part of anterior arch .... 51. *rostratus.*

C. Jaws equal anteriorly; maxillary extending to below eye.
52. *macrostoma.*

1. HAPLOCHROMIS LIVINGSTONII Günth., 1893.

Haplochromis livingstonii (part.) Bouleng. Cat. Afr. Fish. iii. p. 286, fig. 194.

Depth of body $2\frac{3}{5}$ to 3 in length, length of head $2\frac{3}{4}$ to 3. Snout with straight profile, $1\frac{1}{2}$ to 2 diameter of eye, which is $4\frac{1}{4}$ to $5\frac{1}{2}$ in length of head, interorbital width $3\frac{1}{2}$ to 4, depth of præorbital $3\frac{1}{2}$ to 4. Lower jaw projecting; maxillary not extending to below eye; teeth in 3 or 4 series, outer bicuspid and inner tricuspid in young, all conical in adult, 50 to 60 in outer series of upper jaw. 4 or 5 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 to 35 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVI 10–11; last spine $\frac{1}{3}$ to $\frac{2}{5}$ length of head. Anal III 9–10; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral a little shorter than head, reaching origin of anal. Caudal truncate or slightly emarginate. Caudal peduncle longer than deep. Silvery (♀) or bluish grey (♂); a dark bar from eye to end of maxillary; a large opercular spot; body marbled with blackish, the spots and bands constantly nearly as in the figure of the type; pectoral with series of small spots on the rays; dorsal and anal, in male, blackish with pale edge.

The type, 120 mm. long, and three specimens of 200 to 230 mm. (*Wood*).

2. HAPLOCHROMIS POLYSTIGMA, sp. n. (Pl. I.)

Haplochromis livingstonii (part.) Bouleng. Cat. Afr. Fish. iii. p. 286.

Depth of body $2\frac{2}{3}$ to 3 in length, length of head about 3. Snout with straight profile, $1\frac{1}{2}$ to $2\frac{1}{2}$ diameter of eye, which is 4 to 6 in length of head, interorbital width $3\frac{1}{3}$ to 4, depth of præorbital $3\frac{3}{4}$ to $4\frac{1}{2}$. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 3 or 4 series in upper jaw, 2 or 3 in lower, outer bicuspid and inner tricuspid in young, all conical in adult, 50 to 65 in outer series of upper jaw. 4 or 5 series of scales on cheek. 10 to 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 to 34 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 10–11; last spine $\frac{1}{3}$ to $\frac{2}{5}$ length of head. Anal III 9–10; third spine usually a little shorter than last dorsal. Pectoral as long as or a little shorter than head, nearly or quite reaching anal. Caudal truncate or slightly emarginate. Caudal peduncle longer than deep. Body with large irregular brown spots tending to run together to form 3 longitudinal bands; head, body, and vertical fins covered with numerous small dark spots; pectoral with series of spots on the rays.

Six specimens (*Wood*), 120–210 mm. in total length; two others (*Rhoades*, *Cunnington*) also belong to this species.

3. HAPLOCHROMIS MACULIMANUS, sp. n.

Paratilapia modesta (part.) Bouleng. Cat. Afr. Fish. iii. p. 326.

Depth of body $2\frac{2}{5}$ in length, length of head nearly 3. Snout with straight profile, shorter than postorbital part of head. Diameter of eye 5 in length of head, a little less than præorbital depth, $\frac{2}{3}$ depth of cheek; interorbital width 4 in head. Jaws equal anteriorly; maxillary not extending to below eye; teeth conical, in 4 series, about 80 in outer series of upper jaw. 5 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 scales in a longitudinal series, 7 from origin of dorsal to lateral line. Dorsal XVI 11. Anal III 10; third spine $\frac{1}{3}$ head, a little shorter than last dorsal. Caudal peduncle a little longer than deep. Traces of dark cross-bars; pectoral with several transverse series of small dark spots.

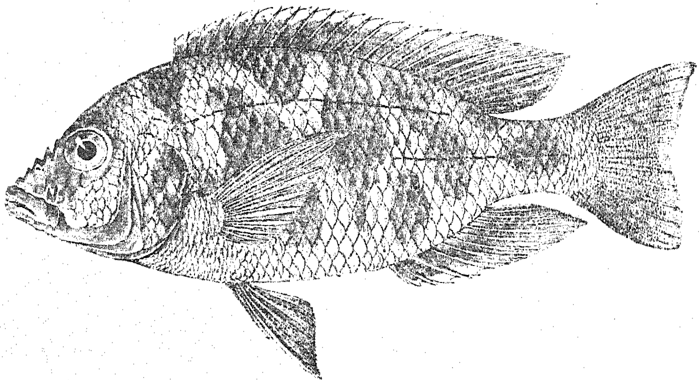
A single specimen, 190 mm. long (*Moore*).

4. HAPLOCHROMIS SIMULANS, sp. n. (Text-fig. 5.)

Depth of body $2\frac{1}{2}$ in the length, length of head 3 to $3\frac{1}{5}$. Snout with straight or convex profile, $1\frac{1}{4}$ to $1\frac{2}{3}$ diameter of eye, which is $3\frac{2}{3}$ to $4\frac{1}{2}$ in length of head, interorbital width 4, depth of præorbital 4 to $4\frac{1}{2}$. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 to 6 series, outer bicuspid, or posteriorly conical in adults, 60 to 75 in outer series of upper jaw. 3 or 4 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 to 34 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVI 10–11; last spine $\frac{1}{3}$ to more than $\frac{2}{5}$ length of head. Anal III 9; third spine as long as last dorsal. Pectoral as long as or a little shorter than head, nearly or quite reaching anal. Caudal truncate or slightly emarginate. Caudal peduncle as long as or a little longer than deep. Silvery or yellowish; a dark bar below eye; an opercular spot; 4 large dark spots on back alternating with 4 very large, vertically expanded spots on side, the spots sometimes confluent to form broad irregular cross-bands; dorsal and anal dusky with yellow margin, or anal pale yellow; caudal dusky above, yellow below.

Four specimens, 130 to 190 mm. in total length (*Wood*).

Text-figure 5.



Haplochromis simulans. $\frac{1}{2}$.

This species bears a great resemblance and is probably closely related to *Cyrtocara venusta*, but differs in the structure of the spinous dorsal fin.

5. Haplochromis subocularis Günth., 1893.

P. Z. S. p. 621, pl. liv. fig. B.

Tilapia johnstoni (part.) Bouleng. Cat. Afr. Fish. iii. p. 249.

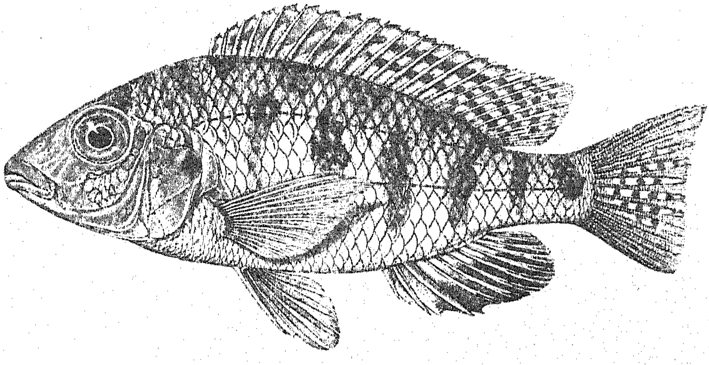
Depth of body 3 to $3\frac{1}{4}$ in length, length of head $3\frac{1}{3}$ to $3\frac{2}{3}$. Snout with straight or slightly convex profile, a little longer than diameter of eye, which is $3\frac{1}{2}$ to $3\frac{3}{4}$ in length of head; interorbital width $3\frac{2}{3}$ to 4 in head, depth of præorbital $4\frac{1}{2}$. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 or 5 series, outer bicuspid, 40 to 50 in outer series of upper jaw. 3 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth enlarged, rounded, blunt. 32 or 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV 11–12; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 8; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral as long as head, nearly or quite reaching anal. Caudal truncate or slightly emarginate. Caudal peduncle $1\frac{1}{2}$ to $1\frac{3}{4}$ as long as deep. Two dark bars across nape; 4 dark spots at base of dorsal alternating with a series above middle of side; 2 large spots on caudal peduncle; dorsal and caudal with series of spots.

Two specimens, 120 and 140 mm. in total length.

6. Haplochromis ornatus, sp. n. (Text-fig. 6.)

Depth of body equal to length of head, $2\frac{3}{4}$ in length of fish. Snout with slightly convex profile, as long as postorbital part of head. Diameter of eye $1\frac{1}{2}$ depth of præorbital, greater than depth of cheek, $3\frac{1}{2}$ in length of head: interorbital width 4 in length of head. Jaws equal anteriorly; lips thick; maxillary not extending to below eye; teeth in 3 series in upper jaw, 4 in the lower; 52 bicuspid teeth in outer series of upper jaw. 3 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth enlarged, rounded, blunt. 31 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 10; spines rather strong, last a little more than $\frac{2}{5}$ length of head. Anal III 9; third spine stronger than dorsals, $\frac{2}{5}$ head. Pectoral nearly as long as head, reaching anal. Caudal feebly emarginate. Caudal peduncle a little longer than deep. Silvery; an opercular spot and a spot above eye; 5 dark spots at base of dorsal alternating with a series above middle of side; 2 dark bars across upper $\frac{1}{2}$ of caudal peduncle; dorsal and caudal with series of spots.

Text-figure 6.



Haplochromis ornatus. $\frac{2}{3}$.

A single specimen, 140 mm. in total length (*Wood*).

7. Haplochromis johnstoni Günth., 1893.

Tilapia johnstoni (part.) Bouleng. Cat. Afr. Fish. iii. p. 249, fig. 167.

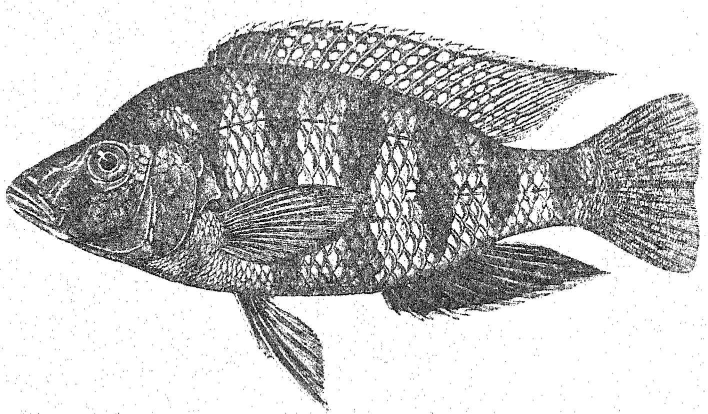
Depth of body $2\frac{3}{4}$ in length, length of head 3. Snout with straight profile, as long as postorbital part of head. Diameter of eye 4 in length of head, interorbital width $4\frac{1}{2}$, depth of præorbital $4\frac{1}{4}$. Lower jaw projecting; maxillary not extending to below eye; teeth in 3 or 4 series, outer bicuspid, 50 in outer series of upper jaw. 3 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, compressed. 31 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 10; last spine a little less than $\frac{1}{3}$ length of head. Anal III 9; third spine stronger than dorsals, nearly $\frac{2}{5}$ head. Pectoral $\frac{4}{5}$ head, reaching origin of anal. Caudal truncate or slightly emarginate. Caudal peduncle $1\frac{1}{3}$ as long as deep. Silvery; a dark bar from eye to angle of mouth; 6 dark bars on body, the first downwards from nape, the fifth from end of dorsal to behind anal; series of spots on dorsal and caudal.

The type, 120 mm. in total length.

8. Haplochromis sexfasciatus, sp. n. (Text-fig. 7.)

Depth of body $2\frac{3}{5}$ to $2\frac{4}{5}$ in the length, length of head 3. Upper profile of head a little concave; snout $1\frac{1}{2}$ to 2 diameter of eye, which is 4 to 5 in length of head, interorbital width $3\frac{2}{3}$ to $4\frac{1}{4}$, præorbital depth 4 to $4\frac{1}{2}$. Lower jaw projecting; maxillary not extending to below eye; teeth in 3 to 5 series, 40 to 60 bicuspid teeth in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Lower pharyngeal with a group of moderately enlarged blunt rounded teeth in the middle posteriorly. 32 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XV 11; last spine $\frac{2}{5}$ to nearly $\frac{1}{2}$ length of head. Anal III 8–9; third spine stronger than last dorsal, $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral $\frac{4}{5}$ to $\frac{7}{8}$ length of head, reaching origin of anal. Caudal truncate or slightly emarginate. Caudal peduncle $1\frac{1}{4}$ as long as deep. Body with 6 blackish cross-bars; dorsal and caudal with series of spots.

Text-figure 7.



Haplochromis sexfasciatus. $\frac{1}{2}$.

Two specimens, 100 and 170 mm. in total length (*Wood*).

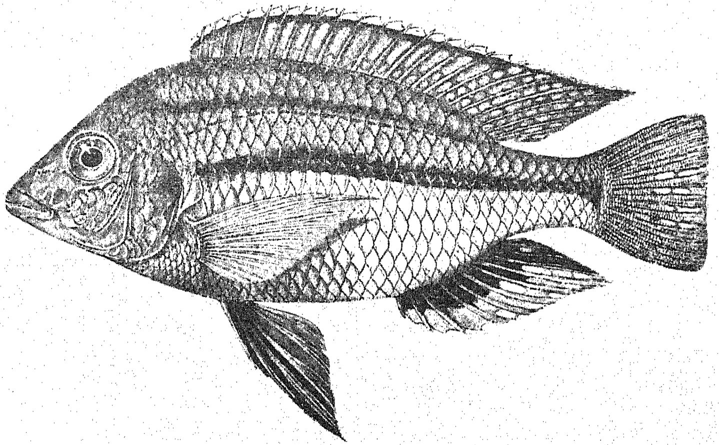
9. HAPLOCHROMIS KIRKII Günth., 1893.

Tilapia kirkii (part.) Bouleng. Cat. Afr. Fish. iii. p. 251, fig. 169.

Depth of body 2½ to 2¾ in length, length of head about 3. Snout with straight profile, 1¼ to 1½ diameter of eye, which is 3¾ to 4¼ in length of head, in adult equal to præorbital depth; interorbital width 3½ to 4¼ in length of head. Lower jaw a little projecting; maxillary extending to between nostril and eye; teeth in 4 or 5 well-separated series, inner tricuspid, outer bicuspid; 40 to 45 in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth stout and blunt. 31 to 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV 10–11; last spine ⅖ to ½ length of head. Anal III 8–10; third spine as long as or a little shorter than last dorsal. Pectoral as long as or a little shorter than head, reaching origin of anal. Caudal truncate or slightly emarginate. Caudal peduncle 1⅓ to 1½ as long as deep. A dark stripe from operculum to caudal. Usually a stripe or a series of spots above upper lateral line and another at base of dorsal; dorsal and caudal with series of spots: anal with ocelli in males.

Seven specimens, 100–160 mm. long (*Johnston*, *Rendall*, *Wood*).

Text-figure 8.



Haplochromis similis. ⅔.

10. HAPLOCHROMIS SIMILIS, sp. n. (Text-fig. 8.)

Depth of body 2½ to 2⅕ in length, length of head 3 to 3⅓. Snout with straight or slightly convex profile, as long as or longer than diameter of eye, which is 3¼ to 3¾ in length of head, greater than præorbital depth; interorbital width 3⅓ to 3⅔ in length of head. Jaws equal anteriorly; maxillary ending between nostril and eye; teeth in 4 to 6 series, outer bicuspid, inner tricuspid, 40 to 52 in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 to 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 or 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI–XVII 9–10; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 9–10; third spine a little shorter than last dorsal. Pectoral as long as or a little shorter than head, nearly or quite reaching anal. Caudal truncate or slightly emarginate. Caudal peduncle $1\frac{1}{4}$ to $1\frac{1}{2}$ as long as deep. Coloration as in *H. kirkii*.

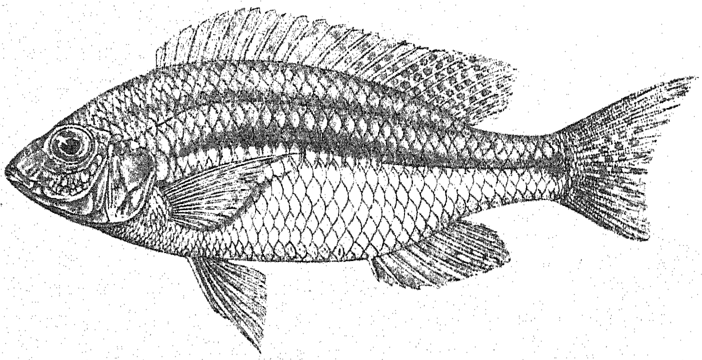
Five specimens, 120–150 mm. long (*Wood*).

11. Haplochromis breviceps, sp. n. (Text-fig. 9.)

Depth of body 3 in the length, length of head $3\frac{2}{3}$. Snout a little shorter or longer than diameter of eye, which is 3 to $3\frac{2}{3}$ in length of head, greater than depth of præorbital or cheek; interorbital width 4 in length of head. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 2 or 3 series; 45 to 60 bicuspid teeth in outer series of upper jaw; 2 series of scales on cheek. 14 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 to 35 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI–XVII 11; last spine $\frac{2}{5}$ length of head. Anal III 9; third spine stronger than dorsals, $\frac{1}{3}$ or a little more than $\frac{1}{3}$ head. Pectoral as long as head, not reaching anal. Caudal emarginate. Caudal peduncle $1\frac{2}{3}$ as long as deep. Silvery; a narrow dusky band from opercular spot to base of caudal, another along upper lateral line, a third at base of dorsal. Dorsal and caudal with series of orange spots; male with ocelli in anal.

Two specimens, 85 and 135 mm. in total length (*Wood*).

Text-figure 9.



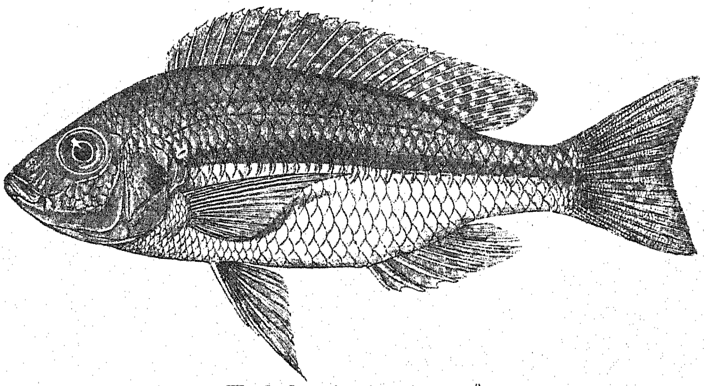
Haplochromis breviceps. $\frac{2}{3}$.

12. Haplochromis microstoma, sp. n. (Text-fig. 10.)

Tilapia kirkii (part.) Bouleng. Cat. Afr. Fish. iii. p. 251.

Depth of body 3 in length, length of head $3\frac{1}{3}$ to $3\frac{1}{2}$. Snout straight, as long as or longer than diameter of eye, which is $3\frac{1}{2}$ to 4 in length of head, a little or considerably greater than præorbital depth; interorbital width 4 in length of head. Mouth small; jaws equal anteriorly; maxillary ending a little behind nostril; teeth in 4 well-separated series, inner tricuspid, outer bicuspid, 24 to 30 in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch.

Text-figure 10.



Haplochromis microstoma. $\frac{3}{4}$.

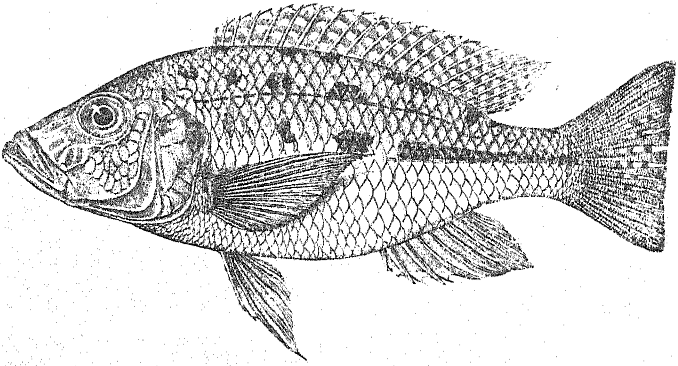
Pharyngeal teeth small. 33 or 34 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVII 11; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 9; third spine a little shorter than last dorsal. Pectoral as long as head, not reaching anal. Caudal deeply emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Silvery; a dark lateral band from operculum to base of caudal; two series of small dark spots, one at base of dorsal, the other above lateral line; dorsal spotted.

Two specimens, 80 mm. (*Wood*) and 115 mm. (*Rhoades*) in length.

13. Haplochromis urotænia, sp. n. (Text-fig. 11.)

Depth of body $2\frac{2}{3}$ to 3 in length, length of head $2\frac{4}{5}$ to 3. Snout with straight upper profile, in adult as long as postorbital part of head. Diameter of eye 4 to $4\frac{1}{2}$ in length of head, equal to or a little less than præorbital depth, less than depth of cheek; interorbital width $3\frac{3}{4}$ to 4 in length of head. Lower jaw a little projecting; maxillary not quite reaching vertical from anterior edge of eye; teeth conical in 2 or 3 series, 35 to 45 in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI 9–10; last spine about $\frac{1}{3}$ length of head. Anal III 8–9; third spine stronger and shorter than last dorsal. Pectoral $\frac{4}{5}$ head, nearly or quite reaching anal.

Text-figure 11.



Haplochromis urotænia. $\frac{3}{7}$.

Caudal truncate or feebly emarginate. Caudal peduncle $1\frac{1}{3}$ to $1\frac{2}{3}$ as long as deep. A series of about 8 dark spots near dorsal profile, a second above lateral line, a third on middle of side posteriorly confluent to form a band; dorsal with series of spots.

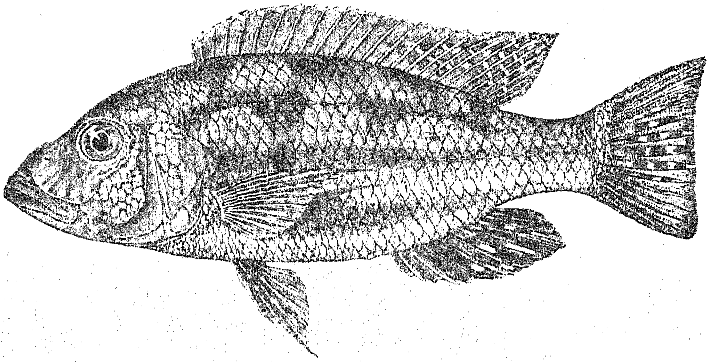
Three specimens, 170 to 200 mm. in total length (*Wood*).

14. HAPLOCHROMIS FUSCOTÆNIATUS, sp. n. (Text-fig. 12.)

Depth of body $2\frac{3}{4}$ in length, length of head $2\frac{3}{4}$. Head $2\frac{1}{2}$ as long as broad. Snout a little concave in front of eye, thence straight, nearly twice as long as diameter of eye, which is 5 in length of head, interorbital width 5, præorbital depth 4. Lower jaw a little projecting; maxillary not quite reaching vertical from anterior edge of eye; teeth conical, in 3 series, 60 in outer series of upper jaw. Cheek with 4 series of scales, depth $1\frac{2}{3}$ diameter of eye. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 34 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 11; spines strongly increasing to last, which is $\frac{1}{3}$ length of head. Anal III 10; third spine stronger and a little shorter than last dorsal. Pectoral $\frac{4}{5}$ head, nearly reaching anal. Caudal truncate. Caudal peduncle $1\frac{1}{3}$ as long as deep. Sides yellowish; a dusky band on middle of side, a second backwards from base of pectoral; a series of dusky spots at base of dorsal, connected with a second series which form an interrupted band on and above lateral line. Dorsal with series of spots. Anal with some pale (? red) round spots.

A single specimen, 175 mm. in total length (*Wood*).

Text-figure 12.



Haplochromis fuscotæniatus. ½.

15. Haplochromis holotænia, sp. n.

Paratilapia dimidiata (part.) Bouleng. Cat. Afr. Fish. iii. p. 360, fig. 244.

Depth of body 3¼ in length, length of head 3. Snout decurved, shorter than postorbital part of head. Diameter of eye 4½ in length of head, equal to interorbital width or præorbital depth, less than depth of cheek. Lower jaw a little projecting; maxillary not extending to below eye; teeth mostly conical, in 4 series in upper jaw and 3 in lower, 60 in outer series of upper jaw. 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 36 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVII 12; last spine $\frac{2}{7}$ head. Anal III 10; third spine stronger and nearly as long as last dorsal. Pectoral $\frac{2}{3}$ length of head. Caudal emarginate. Caudal peduncle 1½ as long as deep. A dark lateral band from eye to base of caudal fin; soft dorsal with series of spots.

A single specimen (*Moore*), 190 mm. in total length.

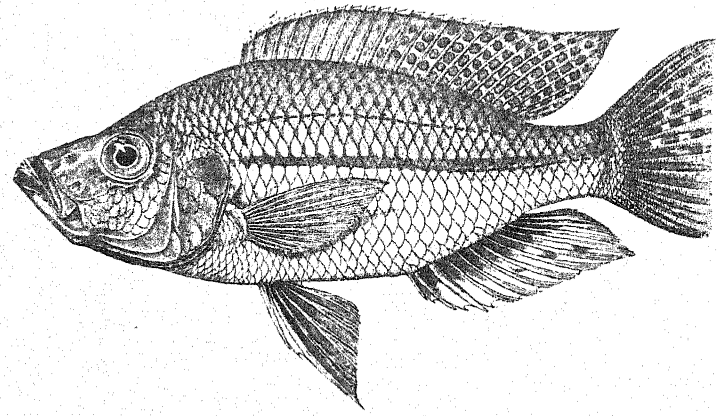
16. Haplochromis strigatus, sp. n. (Text-fig. 13.)

Depth of body 2$\frac{3}{5}$ to 2$\frac{4}{5}$ in length, length of head 2$\frac{4}{5}$ to 3. Snout with straight or slightly concave profile, as long as postorbital part of head. Diameter of eye 4 to 4¼ in length of head, equal to depth of præorbital or interorbital width, less than depth of cheek.

Mouth oblique; lower jaw projecting; maxillary not extending to below eye; teeth conical, triserial, 55 to 60 in outer series of upper jaw. 3 or 4 series of scales on cheek. 12 or 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 or 34 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XV–XVI 11; last spine $\frac{2}{5}$, longest soft rays $\frac{3}{5}$ to $\frac{3}{4}$ length of head. Anal III 10–11; third spine stronger and shorter than last dorsal. Pectoral nearly as long as head, reaching anal. Caudal truncate. Caudal peduncle $1\frac{1}{3}$ as long as deep. Silvery; a blackish stripe, half as broad as a scale, from operculum to base of caudal. Dorsal with series of orange spots; other fins yellowish (♀) or pelvics and anal blackish with red margin (♂).

Three specimens, 170 to 185 mm. in total length (*Wood*).

Text-figure 13.



Haplochromis strigatus. $\frac{1}{2}$.

17. HAPLOCHROMIS DIMIDIATUS Günth., 1864.

Depth of body 4 in length, length of head $3\frac{1}{5}$. Snout with straight upper profile, a little shorter than postorbital part of head. Diameter of eye 5 in length of head, equal to præorbital depth, slightly exceeding interorbital width. Mouth oblique; lower jaw projecting; maxillary ending far in front of eye; teeth conical, in 3 series in upper jaw, 2 in lower; 44 in outer series of upper jaw; anterior teeth of second series in upper jaw enlarged. 3 or 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 35 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 11; last spine $\frac{1}{3}$ length of head. Anal III 11; third spine as long as and stronger than last dorsal. Pectoral $\frac{2}{3}$ length of head. Caudal slightly emarginate.

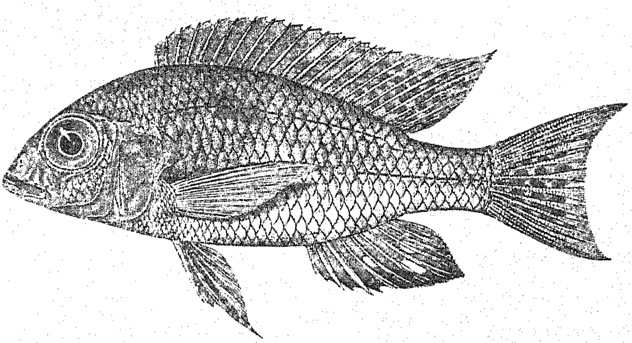
Caudal peduncle twice as long as deep. Silvery; an opercular spot; a blackish lateral stripe, half as broad as a scale, ending in a spot on base of caudal fin.

A specimen of 165 mm. (*Wood*), described above, has been compared with the type, a skin 220 mm. long.

18. HAPLOCHROMIS AURITUS, sp. n. (Text-fig. 14.)

Depth of body $2\frac{4}{5}$ in length, length of head 3. Snout convex, a little shorter than diameter of eye, which is twice præorbital depth, 3 in length of head; interorbital width $4\frac{1}{3}$ in head. Jaws equal anteriorly; maxillary extending to below eye; teeth in 2 series; 66 bicuspid teeth in outer series of upper jaw. 3 series of scales on cheek. 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XV 10; last spine a little less than $\frac{1}{2}$ length of head. Anal III 9; third spine stronger than and nearly as long as last dorsal. Pectoral as long as head, reaching anal. Caudal rather deeply emarginate. Caudal peduncle a little longer than deep. Silvery; a blackish opercular spot; a dark spot on lateral line below spinous dorsal; series of spots on soft dorsal and caudal.

Text-figure 14.



Haplochromis auritus. Nat. size.

A single specimen, 80 mm. in total length (*Wood*).

19. HAPLOCHROMIS TETRASTIGMA Günth., 1893.

Tilapia tetrastigma Bouleng. Cat. Afr. Fish. iii. p. 250, fig. 168.

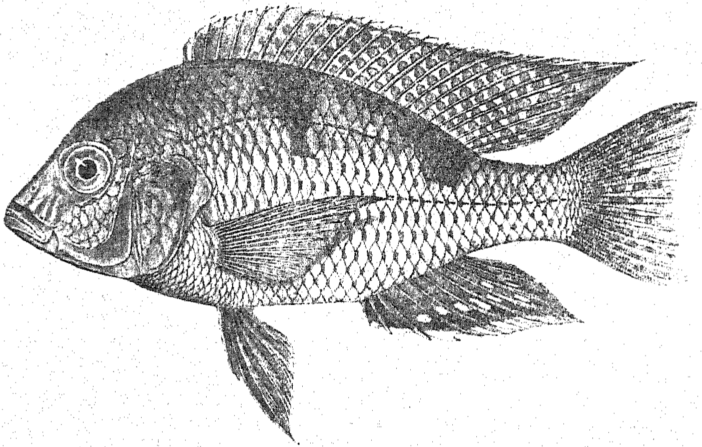
Depth of body $2\frac{1}{2}$ to $2\frac{4}{5}$ in length, length of head about 3. Snout with straight or convex profile, nearly as long as postorbital part of head. Diameter of eye $3\frac{1}{2}$ in length of head, interorbital width 4, præorbital depth 4. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 3 or 4 series, outer bicuspid, about 60 in outer series of upper jaw. 3 or 4 series of scales on cheek. 10 or 11 gill-rakers on lower part of anterior arch. Lower pharyngeal a small weak plate bearing small compressed bicuspid teeth. 30 to 32 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XIV–XV 10–11; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 8–9; third spine a little shorter than last dorsal. Pectoral as long as or a little shorter than head, reaching origin of anal or a little beyond. Caudal slightly emarginate. Caudal peduncle $1\frac{1}{4}$ to $1\frac{1}{2}$ as long as deep. Silvery; four blackish spots, the first on operculum, the second on upper lateral line below spinous dorsal, the third on side below soft dorsal, the fourth at base of caudal.

Three of the types, 105 to 110 mm. in total length.

20. Haplochromis placodon, sp. n. (Text-fig. 15.)

Depth of body $2\frac{1}{3}$ to $2\frac{2}{3}$ in length, length of head about 3. Snout with straight or convex profile, shorter than postorbital part of head. Diameter of eye equal to or greater than depth of præorbital, $3\frac{2}{3}$ to $4\frac{1}{4}$ in length of head, interorbital width $3\frac{1}{3}$ to $3\frac{2}{3}$. Jaws equal anteriorly, lower $\frac{3}{8}$ length of head; maxillary not extending to below eye; teeth in 4 or 5 series, outer bicuspid, 50 to 55 in outer series of upper jaw. 3 or 4 series of scales on cheek. 8 or 9 gill-rakers on lower part of anterior arch. Lower pharyngeal a large and strong plate bearing large rounded flat teeth. 31 to 33 scales in a longitudinal series, 4 or 5 from origin of dorsal to lateral line. Dorsal XVI 10–11;

Text-figure 15.



Haplochromis placodon. $\frac{1}{2}$.

last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 8–9; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral as long as head, extending nearly to middle of anal. Caudal emarginate. Caudal peduncle $1\frac{2}{5}$ to $1\frac{2}{3}$ as long as deep. Silvery; a blackish spot on operculum; two large blackish spots on upper lateral line, expanding upwards towards spinous and soft dorsal; a blackish spot at base of caudal. Dorsal and caudal with series of orange spots; males with a pale edge to dorsal and lower fins dusky, the anal with ocelli.

Five specimens, 130 to 180 mm. in total length (*Wood*).

21. HAPLOCHROMIS INTERMEDIUS Günth., 1864.

Paratilapia intermedia (part.) Bouleng. Cat. Afr. Fish. iii. p. 363.

Depth of body $2\frac{1}{2}$ in length, length of head 3. Snout with straight profile, shorter than postorbital part of head. Diameter of orbit nearly equal to depth of præorbital, which is $4\frac{1}{4}$ in length of head. Jaws equal anteriorly or lower perhaps slightly projecting; lower jaw $\frac{3}{7}$ length of head; præmaxillary pedicels not reaching orbits; maxillary not extending to below eye; teeth small, conical, in 2 or 3 series, about 70 in outer series of upper jaw. 4 series of scales on cheek. 34 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 11; spines strongly increasing to last, which is nearly $\frac{1}{2}$ length of head. Anal III 9; last spine $\frac{1}{3}$ head. Pectoral as long as head, reaching anal. Caudal rather deeply emarginate. Caudal peduncle a little longer than deep. Silvery; traces of two dark spots on upper lateral line; dorsal with series of spots and a pale edge; anal with several spots.

The type, a skin, 185 mm. long.

Boulenger's figure (Cat. Afr. Fish. iii. fig. 247) represents the body and fins correctly, but the head is inaccurate, the præorbital being too narrow; also the four black spots depicted are taken from a specimen of *H. quadrimaculatus.*

H. intermedius is well distinguished from *H. quadrimaculatus* by the deeper præorbital, deeper cheek with 4 series of scales, shorter præmaxillary pedicels, the number of dorsal spines (16 instead of 17 or 18), and the form of the spinous dorsal fin. It shows much closer agreement with *H. placodon*, but has the teeth in fewer series, smaller, and conical instead of cuspidate; also the lower jaw is notably longer.

22. HAPLOCHROMIS MODESTUS Günth., 1893.

Paratilapia modesta (part.) Bouleng. Cat. Afr. Fish. iii. p. 326, fig. 219.

Depth of body 3 in length, length of head $2\frac{3}{5}$. Snout with straight profile, as long as postorbital part of head. Diameter of eye $4\frac{1}{3}$ in length of head, a little greater than præorbital depth, equal to depth of cheek; interorbital width 5 in length of head. Lower jaw projecting; end of maxillary not far short of vertical from anterior edge of eye; teeth conical, in 3 series, 70 in outer series of upper jaw. 4 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 32 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 11; last spine $\frac{1}{3}$ length of head. Anal III 10; third spine stronger and slightly shorter than last dorsal. Pectoral ? Caudal ? (perhaps truncate). Caudal peduncle as long as deep. Colour ?

A single specimen, 150 mm. in total length.

23. HAPLOCHROMIS WOODI, sp. n. (Pl. II.)

Paratilapia modesta (part.) Bouleng. Cat. Afr. Fish. iii. p. 326.

Depth of body $2\frac{1}{2}$ to 3 in length, length of head $2\frac{3}{5}$ to $2\frac{3}{4}$. Snout with straight profile, as long as postorbital part of head. Diameter of eye $3\frac{1}{2}$ to 4 in length of head, equal to or greater than depth of præorbital or cheek; interorbital width 6 to 7 in head. Lower jaw projecting; maxillary not extending to below eye; teeth conical, in 3 or 4 series, 55 to 70 in outer series of upper jaw. 3 or 4 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 32 or 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 9–10; last spine $\frac{1}{3}$ to $\frac{2}{5}$, longest soft rays $\frac{1}{2}$ to $\frac{2}{3}$ length of head. Anal III 9–10; third spine stronger than and about as long as last dorsal. Pectoral a little shorter than head, reaching anal. Caudal truncate or slightly emarginate, angles sometimes rounded. Caudal peduncle as long as or a little longer than deep. Silvery; about 10 faint dark cross-bars; an opercular spot; a series of small dark spots near dorsal profile; a large dark spot on side below spinous dorsal, a second below soft dorsal, a third at base of caudal. Dorsal and caudal with series of orange spots; in males dorsal with blackish intramarginal band and orange edge; pelvics and anal blackish, latter with orange spots.

Six specimens, 130 to 210 mm. long (*Wood*); two in poor condition (*Rendall*) also belong to this species.

24. HAPLOCHROMIS CHRYSONOTUS Bouleng., 1908.

Paratilapia chrysonota Bouleng. Cat. Afr. Fish. iii. p. 362, fig. 246.

Depth of body $2\frac{1}{2}$ to 3 in length, length of head 3 to $3\frac{1}{4}$. Snout with straight profile, as long as or a little shorter than diameter of eye, which is about twice depth of præorbital, $2\frac{3}{4}$ to $3\frac{1}{4}$ in length of head, interorbital width about $3\frac{1}{2}$. Jaws equal anteriorly; præmaxillary pedicels extending to between anterior edges of orbits, $\frac{1}{3}$ length of head; maxillary not extending to below eye; teeth small, conical, in 3 or 4 series. 2 or 3 series of scales on cheek. 18 to 21 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 31 to 34 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 9–11; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 9–11; third spine about $\frac{2}{5}$ head. Pectoral as long as head, reaching anal. Caudal scaly, slightly emarginate. Caudal peduncle as long as or a little longer than deep. Silvery with four blackish spots, one on operculum, the second on and under lateral line below spinous dorsal, the third below soft dorsal, the fourth at base of caudal; males usually darker, often with yellow back.

Several specimens, 100 to 130 mm. long.

25. HAPLOCHROMIS QUADRIMACULATUS, sp. n.

Paratilapia intermedia (part.) Bouleng. Cat. Afr. Fish. iii. p. 363.

Depth of body $2\frac{1}{3}$ to $2\frac{2}{3}$ in length, length of head 3 to $3\frac{1}{2}$. Snout with straight profile, shorter than postorbital part of head. Diameter of eye 4 to $4\frac{1}{2}$ in length of head, depth of præorbital 5 to $5\frac{1}{2}$, interorbital width $3\frac{1}{2}$. Jaws equal or lower slightly projecting; præmaxillary pedicels extending to between anterior edges of orbits, $\frac{2}{5}$ length of head; maxillary not extending to below eye; teeth small, conical, in 2 or 3 series. 2 or 3 series of scales on cheek. 24 to 27 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 34 to 36 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVII–XVIII 11–12; spines equal or slightly increasing from seventh or eighth, last $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 10–12; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral as long as or shorter than head, not or barely reaching anal. Caudal scaly, emarginate. Caudal peduncle a little longer than deep. A blackish spot on operculum, a second under lateral line below spinous dorsal, usually a third between lateral lines and a fourth at base of caudal.

Seven specimens (*Rhoades*, *Whyte*), 170 to 200 mm. long.

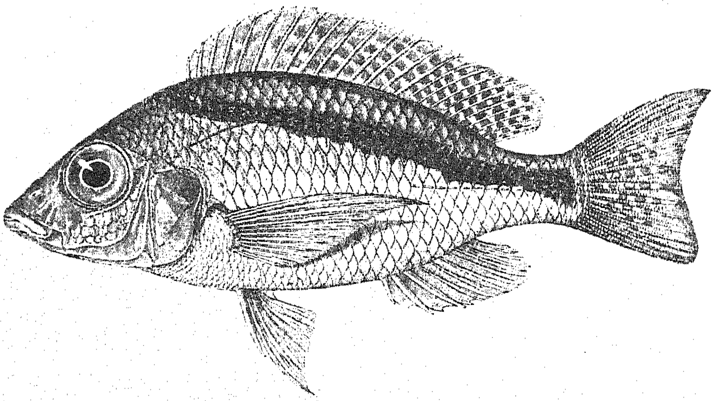
26. HAPLOCHROMIS SPHÆRODON, sp. n. (Text-fig. 16.)

Tilapia lateristriga (part.) Bouleng. Cat. Afr. Fish. iii. p. 253.

Depth of body $2\frac{2}{3}$ to 3 in length, length of head 3 to $3\frac{1}{4}$. Snout with straight profile, as long as or a little shorter than diameter of eye, which is 3 to $3\frac{1}{3}$ in length of head, interorbital width 4, præorbital depth 5. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 to 6 series, 40 to 60 bicuspid teeth in outer series of upper jaw. 2 to 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. Middle pharyngeal teeth large, with spherical crowns. 31 or 32 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XV–XVI 10–12; last spine about $\frac{2}{5}$ length of head. Anal III 8–9; third spine usually a little shorter than last dorsal. Pectoral about as long as head, reaching anal. Caudal slightly emarginate. Caudal peduncle 1¼ to 1½ as long as deep. An opercular spot; a blackish band from nape to caudal.

Five specimens, 80 to 125 mm. long (*Wood*, *Rhoades*), and a skeleton.

Text-figure 16.

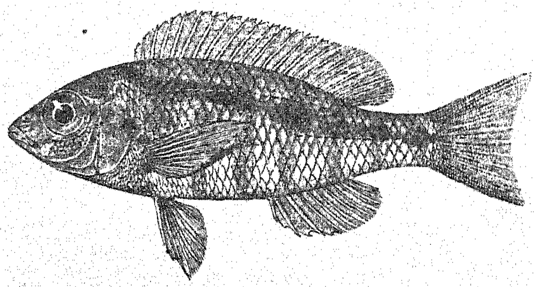


Haplochromis sphærodon. ⅘.

27. Haplochromis ericotænia, sp. n. (Text-fig. 17.)

Depth of body 3¼ to 3½ in length, length of head 3 to 3⅓. Snout with straight profile, nearly as long as or shorter than diameter of eye, which is 2¾ to 3 in length of head, interorbital

Text-figure 17.



Haplochromis ericotænia. Nat. size.

width 4¼, præorbital depth 5½ to 6. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 series, 35 bicuspid teeth in outer series of upper jaw. 3 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Middle posterior pharyngeal teeth enlarged and obtuse, probably spherical in adult. 31 scales in a longitudinal series, 7 from origin of dorsal to lateral line. Dorsal XV–XVI 11; last spine ⅖ or a little more than ⅖ length of head. Anal III 9–10; third spine as long as last dorsal. Pectoral ⅘ head, not reaching anal. Caudal slightly emarginate. Caudal peduncle 1⅔ as long as deep. Silvery; an opercular spot; 8 faint dark cross-bars on body; a blackish band, more or less broken up into a series of spots on the bars, from nape to middle of base of caudal.

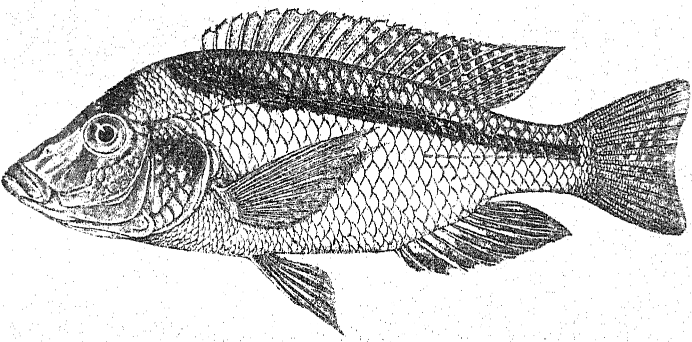
Two specimens, 65 and 72 mm. in total length (*Wood*).

28. HAPLOCHROMIS LATERISTRIGA Günth., 1864. (Text-fig. 18.)

Chromis lateristriga (part.) Günth. P. Z. S. 1864, p. 312.
Tilapia lateristriga (part.) Bouleng. Cat. Afr. Fish. iii. p. 253.
Tilapia lethrinus (part.) Bouleng. t. c. p. 254.

Depth of body 2¾ to 3 in length, length of head 2¾. Snout with straight upper profile, as long as postorbital part of head. Diameter of eye 4 to 5 in length of head, interorbital width 3½ to 4½, depth of præorbital 3½ to 4. Lower jaw a little projecting; maxillary exposed distally, ending below nostril; teeth in 3 or 4 series, inner small; 40 to 55 bicuspid teeth in outer series of upper jaw. Cheek with 3 to 5 series of scales. 13 gill-rakers on lower part of anterior arch. A group of large blunt teeth on posterior part of lower pharyngeal. 34 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XV–XVI 10–11; last spine ⅓ to ⅖ length of head. Anal III 9; third spine stronger and a little shorter than last dorsal. Pectoral ¾ or ⅘ head, nearly or quite reaching anal. Caudal densely scaled, slightly emarginate. Caudal peduncle 1½ as long as deep. A blackish band from in front of dorsal fin to upper part of base of caudal; an opercular spot; dorsal and caudal spotted.

Text-figure 18.



Haplochromis lateristriga. ½.

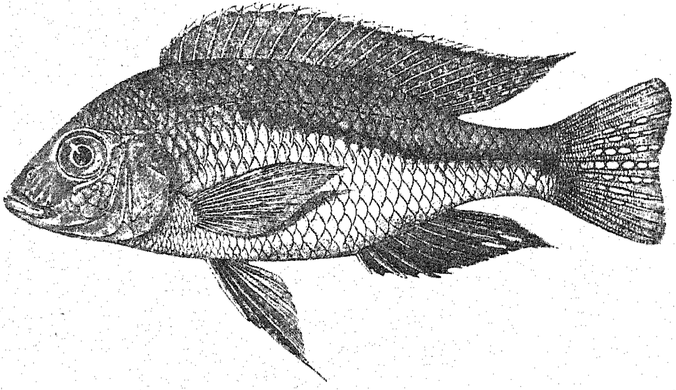
Three specimens: the type, a skin 160 mm. long, a specimen of 185 mm. (*Wood*), and another of 100 mm. (*Rhoades*).

29. HAPLOCHROMIS PLAGIOTÆNIA, sp. n. (Text-fig. 19.)

Tilapia lateristriga (part.) Bouleng. Cat. Afr. Fish. iii. p. 253.

Depth of body $2\frac{2}{3}$ to $3\frac{1}{3}$ in length, length of head 3 to $3\frac{1}{4}$. Snout with straight or slightly convex profile, as long as or a little longer than diameter of eye, which is 3 to 4 in length of head, greater than præorbital depth, equal to or greater than depth of cheek; interorbital width $3\frac{1}{4}$ to $3\frac{3}{4}$ in head. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 2 to 4 series; 35 to 50 bicuspid teeth in outer series of upper jaw. 3 or 4 series of scales on cheek. 8 to 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, compressed, those of the series on each side of middle line a little enlarged. 31 to 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 10–11; last spine about $\frac{1}{2}$ length of head. Anal III 8–9; third spine $\frac{2}{5}$ to $\frac{1}{2}$ head. Soft dorsal, anal, and pelvic fins produced in males. Pectoral as long as or a little shorter than head, nearly or quite reaching anal. Caudal slightly emarginate. Caudal peduncle longer than deep. A dark band from nape to middle of base of caudal; dorsal and caudal usually with series of spots; males darker in colour, with dark fins, the dorsal with a pale edge.

Text-figure 19.



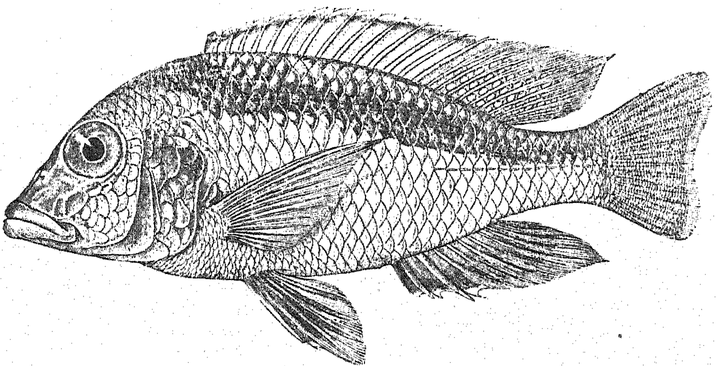
Haplochromis plagiotænia. ♀.

17 specimens, 70 to 110 mm. in total length (*Rhoades*, *Wood*), all but one with 15 dorsal spines.

30. HAPLOCHROMIS MELANOTÆNIA, sp. n. (Text-fig. 20.)

Depth of body $2\frac{2}{3}$ to $2\frac{3}{4}$ in length, length of head $2\frac{3}{4}$ to 3. Snout straight, declivous, nearly as long as or a little longer than diameter of eye, which is 3 to $3\frac{1}{2}$ in length of head, equal to or greater than interorbital width, greater than præorbital depth, not less than depth of cheek. Jaws equal anteriorly; maxillary extending to below anterior edge of eye; lips thick; teeth in 4 or 5 well-separated series, conical, or outer bicuspid and inner tricuspid in young, 40 to 50 in outer series of upper jaw. 3 or 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. Lower pharyngeal stout; middle teeth conical or slightly compressed, moderately strong, set well apart, only 8 in the series on each side of middle line. 33 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XV–XVII 10–11; last spine about $\frac{2}{5}$ length of head. Anal III 9; third spine stronger than dorsals, $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral as long as head, reaching anal. Caudal truncate or slightly emarginate. Caudal peduncle $1\frac{1}{3}$ to $1\frac{2}{3}$ as long as deep An opercular spot; a blackish band from nape to caudal; series of orange spots on dorsal.

Text-figure 20.



Haplochromis melanotænia. $\frac{1}{2}$.

Three specimens, 120 to 170 mm. in total length (*Wood*).

31. HAPLOCHROMIS GUENTHERI, sp. n.

Chromis lateristriga (part.) Günth. P. Z. S. 1864, p. 312.

Tilapia lateristriga (part.) Bouleng. Cat. Afr. Fish. iii. p. 253, fig. 170.

Paratilapia dimidiata (part.) Bouleng. t. c. p. 360.

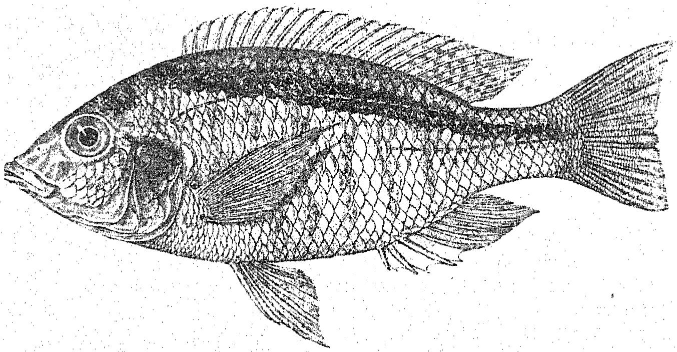
Depth of body $2\frac{1}{2}$ to 3 in length, length of head $3\frac{1}{3}$ to $3\frac{1}{2}$. Snout with straight or slightly convex profile, shorter than postorbital part of head. Diameter of eye $3\frac{1}{2}$ to 5 in length of head, greater (young) or less (adult) than depth of præorbital, less than depth of cheek; interorbital width about 4 in length of head. Lower jaw a little shorter than upper; maxillary not extending to below eye; teeth in 3 or 4 series, outer bicuspid in young, conical in adult, 40 to 70 in outer series of upper jaw; anterior outer teeth of lower jaw directed outwards. 3 or 4 series of scales on cheek. 13 or 14 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, none enlarged. 33 to 35 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI–XVII 10–12; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head. Anal III 8–10; third spine stronger and shorter than last dorsal. Pectoral as long as head, usually not reaching anal. Caudal slightly emarginate. Caudal peduncle longer than deep. Silvery; an opercular spot; a blackish band from nape to caudal; usually a series of dark spots at base of dorsal; series of orange spots on dorsal fin.

Seven specimens of 130 to 190 mm. (*Wood*), the one figured by Boulenger (*Rhoades*), and one of the types of *C. lateristriga* a skin 245 mm. long.

32. HAPLOCHROMIS MELANONOTUS, sp. n. (Text-fig. 21.)

Depth of body $2\frac{3}{5}$ to 3 in length, length of head $3\frac{1}{4}$. Profile of head evenly decurved. Snout $\frac{7}{8}$ to $1\frac{1}{3}$ diameter of eye, which is 3 to $3\frac{3}{4}$ in length of head, greater than depth of præorbital or cheek; interorbital width $3\frac{1}{4}$ to 4 in head. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 or 5 series; 40 to 60 biscuspid teeth in outer series of upper jaw. 4 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, none enlarged. 34–35 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVIII–XIX 10; last spine $\frac{2}{5}$ to $\frac{1}{2}$ length of head, longest soft rays $\frac{1}{2}$ head. Anal III 10; third spine from less than $\frac{1}{3}$ to more than $\frac{2}{5}$ head. Pectoral as long as or a little shorter than head, nearly or quite reaching anal. Caudal slightly emarginate. Caudal peduncle $1\frac{1}{3}$ as long as deep. Silvery; a blackish band from nape to upper half of base of caudal.

Text-figure 21.



Haplochromis melanonotus. $\frac{3}{7}$.

Two specimens, 85 and 200 mm. in total length (*Wood*).

33. HAPLOCHROMIS BREVIS Bouleng., 1908.

Tilapia brevis Bouleng. Cat. Afr. Fish. iii. p. 262, fig. 177.

Depth of body $2\frac{1}{2}$ in length, length of head $2\frac{2}{3}$. Snout convex, shorter than diameter of eye, which is twice præorbital depth, $2\frac{1}{2}$ to $2\frac{2}{3}$ in length of head; interorbital width 4 in head. Jaws equal anteriorly; maxillary extending to below anterior edge of eye; teeth in 2 or 3 series; 65 to 80 bicuspid teeth in outer series of upper jaw. 3 series of scales on cheek. 8 or 9 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 31 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XV 12; last spine a little less than $\frac{1}{2}$ length of head. Anal III 9; third spine stronger than dorsals, $\frac{3}{5}$ head. Pectoral as long as head, reaching anal. Caudal emarginate. Caudal peduncle as long as deep. Silvery; an opercular spot; a dark band from nape to base of caudal.

Two specimens, 70 and 75 mm. in total length.

34. HAPLOCHROMIS NOTOTÆNIA Bouleng., 1902.

Paratilapia nototænia Bouleng. Cat. Afr. Fish. iii. p. 359.

Depth of body $2\frac{2}{3}$ to 3 in length, length of head $2\frac{3}{4}$ to 3. Snout decurved, shorter than postorbital part of head. Diameter of eye $3\frac{3}{4}$ to $4\frac{1}{3}$ in length of head, interorbital width $3\frac{1}{3}$ to $3\frac{1}{2}$, præorbital depth 4 to $4\frac{1}{2}$. Jaws equal anteriorly; maxillary extending to below anterior margin of eye; teeth in 3 to 5 series, outer biscuspid in young, conical in adult, 75 to 90 in outer series of upper jaw. 3 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 35 or 36 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI–XVII 10–12; last spine $\frac{1}{3}$ length of head. Anal III 9–10; third spine $\frac{1}{4}$ to $\frac{2}{7}$ head. Pectoral a little shorter than head, reaching origin of anal. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. An opercular spot; a blackish band on each side of back from origin of dorsal to caudal; dorsal and caudal with bars or series of spots; lower fins tinged with orange.

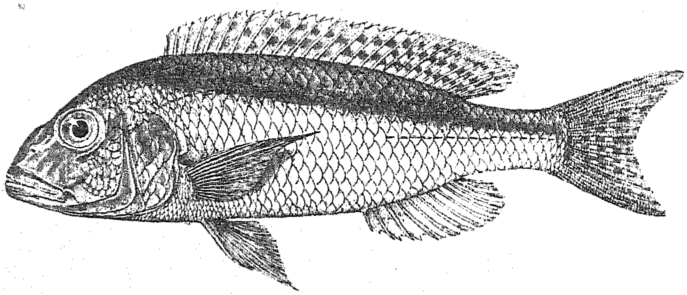
The type and three specimens of 180 to 250 mm. (*Wood*).

35. HAPLOCHROMIS LEPTURUS, sp. n. (Text-fig. 22.)

Paratilapia rhoadesii (part.) Bouleng. Cat. Afr. Fish. iii. p. 361.

Depth of body $3\frac{1}{5}$ to $3\frac{3}{5}$ in length, length of head 3 to $3\frac{1}{2}$. Snout decurved, a little shorter than postorbital part of head. Diameter of eye $4\frac{1}{3}$ to 6 in length of head, interorbital width $3\frac{2}{3}$ to 4, depth of præorbital 4 to $4\frac{1}{3}$. Jaws equal anteriorly; maxillary extending to vertical from anterior edge of eye; teeth conical, in 3 to 6 series, 70 to 90 in outer series of upper jaw. 4 or 5 series of scales on cheek. 11 to 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, 37 to 39 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVII 11–13; last spine from a little less than $\frac{1}{3}$ to nearly $\frac{2}{5}$ length of head. Anal III 10–11; third spine stronger and a little shorter than last dorsal. Pectoral $\frac{3}{4}$ to $\frac{7}{8}$ length of head, not reaching anal. Caudal emarginate. Caudal peduncle $1\frac{2}{3}$ to 2 as long as deep. Silvery; back darker; an opercular spot; a dark band from origin of dorsal to caudal (absent in the largest specimen, which is darker than the others); series of spots on dorsal.

Text-figure 22.



Haplochromis lepturus. $\frac{4}{5}$.

Five specimens of 170 to 240 mm. (*Wood*) and one of 360 mm. (*Rhoades*).

36. HAPLOCHROMIS RHOADESII Bouleng., 1908.

Paratilapia rhoadesii (part.) Bouleng. Cat. Afr. Fish. iii. p. 361, fig. 245.

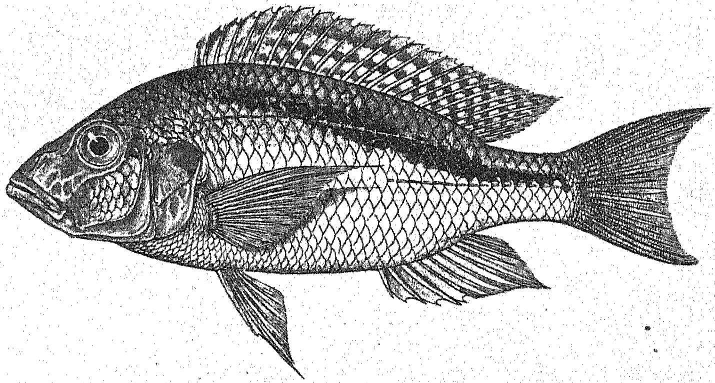
Depth of body $2\frac{3}{5}$ to 3 (adult) or $3\frac{2}{5}$ (young) in the length, length of head $2\frac{4}{5}$ to 3. Snout decurved, as long as postorbital part of head. Diameter of eye 4 to $5\frac{1}{2}$ in length of head, interorbital width 4 to $4\frac{1}{2}$, depth of præorbital $3\frac{1}{2}$ to $4\frac{1}{2}$. Lower jaw usually a little projecting; maxillary not extending to below eye; teeth cuspidate in young, conical in adult, in 3 to 5 series, 60 to 80 in outer series of upper jaw. 4 or 5 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 35 to 37 scales in a longitudinal series, 5 to 7 from origin of dorsal to lateral line. Dorsal XV–XVII 11–13; spines equal or slightly increasing from sixth or seventh, last $\frac{1}{4}$ to $\frac{1}{3}$ length of head. Anal III 10; third spine stronger than dorsals, $\frac{1}{4}$ to $\frac{1}{3}$ head. Pectoral $\frac{3}{4}$ to $\frac{7}{8}$ head, reaching vent or origin of anal. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ to $1\frac{2}{3}$ as long as deep. An opercular spot; body with or without faint dark cross-bars; a blackish band from nape to caudal; dorsal with series of spots.

The type (250 mm.) and a series of specimens 120 to 250 mm. long (*Wood*).

37. HAPLOCHROMIS ATRITÆNIATUS, sp. n. (Text-fig. 23.)

Depth of body 2$\frac{2}{3}$ in length, length of head 3. Snout with straight profile, nearly as long as postorbital part of head. Diameter of eye 4 to 4$\frac{1}{2}$ in length of head, interorbital width 4, depth of præorbital 4 to 4$\frac{1}{2}$. Lower jaw slightly projecting; maxillary not quite reaching vertical from anterior edge of eye; teeth in 3 series, outer bicuspid or some conical, 70 in outer series of upper jaw. 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 or 34 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVI 10–11; spines equal or slightly increasing from the sixth, last $\frac{2}{5}$ or a little more than $\frac{2}{5}$ length of head.

Text-figure 23.



Haplochromis atritæniatus. $\frac{1}{2}$.

Anal III 9; third spine $\frac{1}{3}$ head. Pectoral as long as head, extending a little beyond origin of anal. Caudal emarginate. Caudal peduncle 1$\frac{1}{2}$ to 1$\frac{2}{3}$ as long as deep. An opercular spot; a blackish band from nape to caudal; dorsal and caudal with series of spots.

Two specimens, 150 and 170 mm. long (*Wood*).

38. HAPLOCHROMIS SPILORHYNCHUS, sp. n. (Pl. VI. fig. 2.)

Paratilapia dimidiata (part.) Bouleng. Cat. Afr. Fish. iii. p. 360.

Depth of body 3$\frac{1}{5}$ to 3$\frac{2}{3}$ in length, length of head about 3. Snout decurved, as long as postorbital part of head. Diameter of eye 4$\frac{2}{3}$ to 5$\frac{1}{2}$ in length of head, less than depth of præorbital or cheek; interorbital width 4$\frac{2}{3}$ to 5$\frac{1}{2}$ in length of head. Lower jaw a little projecting; maxillary not extending to below eye; teeth conical, in 3 or 4 series, outer strong and spaced, 25 to 40 in upper jaw. 5 or 6 series of scales on cheek. 10 or 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 36 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVI 12; last spine $\frac{1}{3}$ length of head. Anal III 9–10; third spine as long as and stronger than last dorsal. Pectoral $\frac{3}{4}$ to $\frac{4}{5}$ head, not reaching anal. Caudal emarginate. Caudal peduncle $1\frac{2}{3}$ as long as deep. A large black spot on præorbital; an opercular spot; a blackish band on each side of back from origin of dorsal to caudal.

Seven specimens (*Wood*, *Rhoades*, *Rendall*) 150–240 mm. in total length.

39. Haplochromis longipes, sp. n. (Pl. V. fig. 2.)

Depth of body $3\frac{1}{2}$ in length, length of head 3. Snout decurved, twice as long as diameter of eye, which is $5\frac{1}{2}$ in length of head, less than depth of præorbital or cheek; interorbital width $4\frac{2}{3}$ in length of head. Lower jaw a little projecting; maxillary not quite reaching vertical from anterior edge of eye. Teeth conical, in 3 series, outer rather strong, 45 in upper jaw. 5 series of scales on cheek; 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 37 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 12; spines strongly increasing to last, which is $\frac{2}{5}$ length of head. Anal III 10; third spine $\frac{2}{7}$ length of head. Soft dorsal and anal produced, pointed. Pectoral $\frac{3}{4}$ length of head; pelvics as long as head. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. An opercular spot; a blackish band on each side of back from nape to base of caudal.

A single specimen, 260 mm. in total length.

40. Haplochromis cæruleus Bouleng., 1908.

Champsochromis cœruleus Bouleng. Cat. Afr. Fish. iii. p. 433, fig. 295.

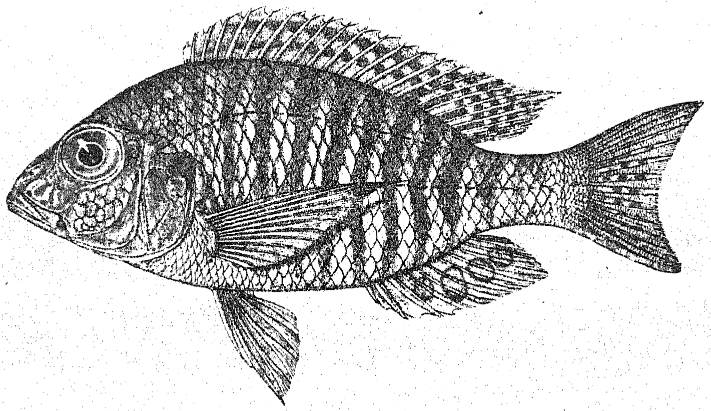
Closely related to the preceding, differing as follows:—Depth of body 4 in length, head $3\frac{1}{4}$. Snout $2\frac{1}{2}$ diameter of eye, which is 6 in length of head. Interorbital width 4 in head. Maxillary not nearly reaching vertical from anterior edge of eye. 11 gill-rakers on lower part of anterior arch. Caudal peduncle twice as long as deep.

Total length 255 mm.

41. Haplochromis macrochir, sp. n. (Text-fig. 24.)

Depth of body $2\frac{2}{5}$ in length, length of head nearly 3. Snout with straight or slightly convex profile, as long as diameter of eye, which is $3\frac{1}{4}$ in length of head, $1\frac{1}{3}$ depth of præorbital or cheek; interorbital width 4 to $4\frac{1}{3}$ in head. Jaws equal anteriorly; maxillary extending to vertical from anterior edge of eye; teeth very small, in 2 or 3 series, outer bicuspid, about 80 in outer series of upper jaw; 4 series of scales on cheek. 13 or 14 gill-rakers on lower part of anterior arch. A group of enlarged teeth with spherical crowns on posterior half of lower pharyngeal. 33 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 10; last spine $\frac{2}{5}$ to $\frac{1}{2}$, longest soft rays $\frac{2}{3}$ to $\frac{4}{5}$ length of head. Anal III 9; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral longer than head, reaching middle of anal. Caudal emarginate. Caudal peduncle longer than deep. Silvery; an opercular spot; about 10 faint dark cross-bars; dorsal and caudal with series of spots; anal, in male, with several ocelli.

Text-figure 24.



Haplochromis macrochir. $\frac{2}{3}$.

Two specimens, 115 and 130 mm. long (*Wood*).

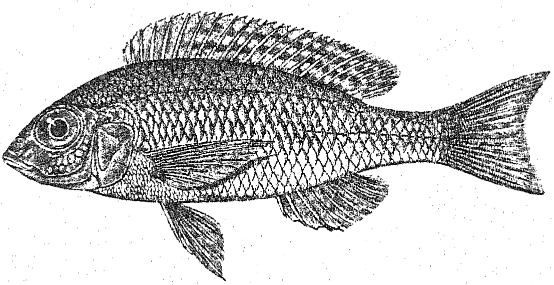
42. HAPLOCHROMIS ARGYROSOMA, sp. n. (Text-fig. 25.)

Tilapia macrophthalma (part.) Bouleng. Cat. Afr. Fish. iii. p. 261.

Depth of body equal to length of head, $3\frac{1}{5}$ in length of fish. Snout decurved, shorter than diameter of eye, which is 3 in length of head, twice depth of præorbital or cheek; interorbital width 5 in length of head. Jaws equal anteriorly; maxillary extending to below anterior edge of eye; teeth in 2 or 3 series, 50 in outer series of upper jaw, mostly bicuspid, but the last few on each side conical; 2 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Last few teeth of two middle series of lower pharyngeal enlarged. 33 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVII 10; last spine nearly $\frac{1}{2}$ length of head. Anal III 9; third spine less than $\frac{2}{5}$ head. Pectoral as long as head, reaching anal. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Silvery; dorsal and caudal with series of spots.

A single specimen, one of the types of *T. macrophthalma*, 75 mm. in total length.

Text-figure 25.



Haplochromis argyrosoma. Nat. size.

43. Haplochromis macrophthalmus Bouleng., 1908.

Tilapia macrophthalma (part.) Bouleng. Cat. Afr. Fish. iii. p. 261, fig. 176.

Depth of body $2\frac{2}{3}$ to 3 in length, length of head 3. Snout with slightly convex profile, shorter than diameter of eye, which is $2\frac{1}{2}$ in length of head, twice depth of præorbital or cheek, or interorbital width. Lower jaw a little shorter than upper; maxillary not extending to below eye; teeth in 2 series, 50 or 60 bicuspid teeth in outer series of upper jaw, anterior outer teeth of lower jaw directed outwards. 2 series of scales on cheek. 12 or 13 gill-rakers on lower part of anterior arch. Last few teeth of 2 middle series of lower pharyngeal a little enlarged. 32 or 33 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 10; last spine nearly $\frac{1}{2}$ length of head. Anal III 8; third spine as long as last dorsal. Pectoral a little longer than head, extending to above anal. Caudal emarginate. Caudal peduncle $1\frac{1}{3}$ as long as deep. Silvery.

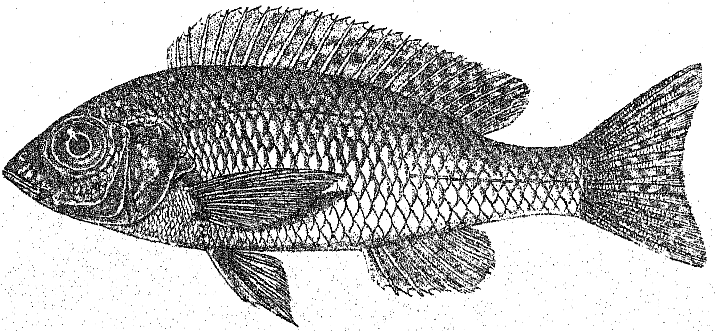
Four specimens, 70 to 80 mm. in total length (*Rhoades*).

44. Haplochromis leuciscus, sp. n. (Text-fig. 26.)

Depth of body $3\frac{1}{4}$ to $3\frac{1}{3}$ in length, length of head $3\frac{1}{4}$ to $3\frac{1}{3}$. Snout with straight or slightly convex profile, a little shorter than diameter of eye, which is 3 in length of head, twice præorbital depth; interorbital width $4\frac{1}{2}$ in head. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 2 or 3 series; 45 bicuspid teeth in outer series of upper jaw. 2 or 3 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 31 to 33 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI-XVII 11; last spine $\frac{2}{5}$ length of head. Anal III 9; third spine stronger and as long as or a little shorter than last dorsal. Pectoral $\frac{4}{5}$ to $\frac{7}{8}$ head, not reaching anal. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Silvery; dorsal and caudal with series of spots.

Two specimens, 75 and 80 mm. long (*Rhoades*, *Wood*).

Text-figure 26.



Haplochromis leuciscus. Nat. size.

45. HAPLOCHROMIS INORNATUS Bouleng., 1908.

Tilapia inornata Bouleng. Cat. Afr. Fish. iii. p. 263, fig. 178.

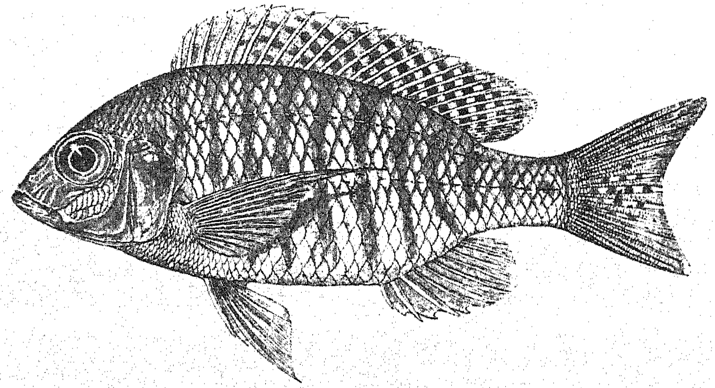
Depth of body $3\frac{1}{4}$ to $3\frac{1}{3}$ in length, length of head $3\frac{1}{4}$. Snout shorter than diameter of eye, which is $2\frac{3}{4}$ to 3 in length of head and twice depth of præorbital or cheek; interorbital width $4\frac{1}{4}$ in length of head. Jaws equal anteriorly; maxillary not extending to below eye; teeth small, in 3 series; 50 bicuspid teeth in outer series of upper jaw. 2 or 3 series of scales on cheek. 15 or 16 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 34 to 36 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI–XVIII 11–12; last spine $\frac{2}{5}$ length of head. Anal III 9; third spine nearly as long as last dorsal. Pectoral as long as head, not reaching anal. Caudal emarginate. Caudal peduncle $1\frac{2}{3}$ as long as deep. Silvery.

Two specimens, 85 and 95 mm. in total length (*Rhoades*).

46. HAPLOCHROMIS MICRENTODON, sp. n. (Text-fig. 27.)

Depth of body $2\frac{1}{2}$ to $2\frac{2}{3}$ in length, length of head $3\frac{1}{4}$ to $3\frac{1}{3}$. Snout with slightly convex profile, a little shorter than diameter of eye, which is 3 in length of head, $1\frac{2}{3}$ præorbital depth, $1\frac{1}{2}$ depth of cheek; interorbital width 4 in length of head. Lower jaw a little shorter than upper; maxillary not extending to below eye; teeth in 2 or 3 series, outer bicuspid, about 70 in upper jaw; inner teeth of lower jaw minute, almost invisible, outer anterior teeth directed outwards. 2 or 3 series of scales on cheek. 16 or 17 gill-rakers on lower part of anterior arch. Pharyngeal teeth very small. 33 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 10–11; last spine $\frac{2}{5}$ to $\frac{1}{2}$, longest soft rays $\frac{1}{2}$ to $\frac{3}{5}$ length of head. Anal III 8–9; third spine a little shorter than last dorsal. Pectoral longer than head, extending beyond origin of anal. Caudal emarginate. Caudal peduncle longer than deep. Silvery, with traces of several dark cross-bars; dorsal and caudal with series of spots.

Text-figure 27.



Haplochromis micrentodon. $\frac{4}{5}$.

Two specimens, 110 and 115 mm. long (*Wood*).

47. Haplochromis eucinostomus, sp. n. (Pl. IV. fig. 1.)

Depth of body $3\frac{1}{3}$ to $3\frac{1}{2}$ in length, length of head $3\frac{1}{3}$. Snout with straight profile, as long as diameter of eye, which is $3\frac{1}{3}$ in length of head, much greater than præorbital depth; interorbital width $3\frac{1}{4}$ to $3\frac{1}{2}$ in length of head. Mouth small, oblique; jaws equal anteriorly; præmaxillary pedicels extending to between middle of orbits, $\frac{2}{5}$ length of head; maxillary not extending to below eye; teeth small, in 2 or 3 series, outer bicuspid. 3 series of scales on cheek. 16 or 17 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender. 35 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI–XVII 11–12; last spine $\frac{2}{5}$ length of head. Anal III 10; third spine stronger than dorsals, $\frac{1}{3}$ head. Pectoral a little shorter than head, not reaching anal. Caudal emarginate, densely scaled in basal half. Caudal peduncle $1\frac{1}{2}$ as long as deep. Silvery, with traces of dark cross-bars.

Two specimens, 85 and 100 mm. long (*Wood*), the smaller (? ♂) much darker in colour than the larger.

48. HAPLOCHROMIS PRÆORBITALIS, sp. n. (Pl. III.)

Depth of body $2\frac{2}{3}$ to $2\frac{3}{4}$ in length, length of head $2\frac{3}{4}$–3. Snout longer than postorbital part of head; upper profile straight, obliquely descending. Diameter of eye 5 in length of head, interorbital width $4\frac{1}{2}$, depth of præorbital 3. Lower jaw projecting; maxillary ending not far behind nostril; teeth in 3 series in upper jaw, 4 in lower, outer bicuspid, about 70 in upper jaw. 4 series of scales on cheek. 9 or 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender. 35 or 36 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XV–XVI 12–13; last spine $\frac{2}{5}$ or $\frac{1}{2}$ length of head; longest soft rays $\frac{3}{5}$ or $\frac{3}{4}$ head. Anal III 10–11; third spine stronger than dorsals, $\frac{2}{7}$ or $\frac{1}{3}$ head. Pectoral a little shorter than head, reaching anal. Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Greyish; an opercular spot; dorsal with oblique stripes or series of spots.

Two specimens, 210 and 240 mm. in total length (*Wood*). The larger has the dorsal fin higher than the other and the lower fins dusky; it is probably a male.

49. HAPLOCHROMIS COMPRESSICEPS Bouleng., 1908.

Paratilapia compressiceps Bouleng. Cat. Afr. Fish. iii. p. 331, fig. 222.

Depth of body 3 in length, length of head $2\frac{3}{5}$ to $2\frac{3}{4}$. Head 4 times as long as broad; snout a little concave in front of eye, thence straight, longer than postorbital part of head. Diameter of eye $5\frac{1}{2}$ to 6 in length of head, equal to interorbital width, from a little more than $\frac{1}{2}$ to nearly $\frac{2}{3}$ depth of præorbital. Lower jaw projecting; chin deep; maxillary ending a little behind nostril; teeth conical, in 3 series. 3 or 4 series of scales on cheek. 11 to 13 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 to 35 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 11–13; last spine $\frac{1}{3}$ length of head. Anal III 10–11; third spine as long as last dorsal. Caudal scaly, truncate. Caudal peduncle $1\frac{1}{2}$ to $1\frac{3}{4}$ as long as deep. Silvery; three yellow-green bands, one along upper outline of head and body, the second above upper lateral line, the third along middle of side.

The type, 160 mm. long, and 3 specimens of 180–200 mm. (*Wood*).

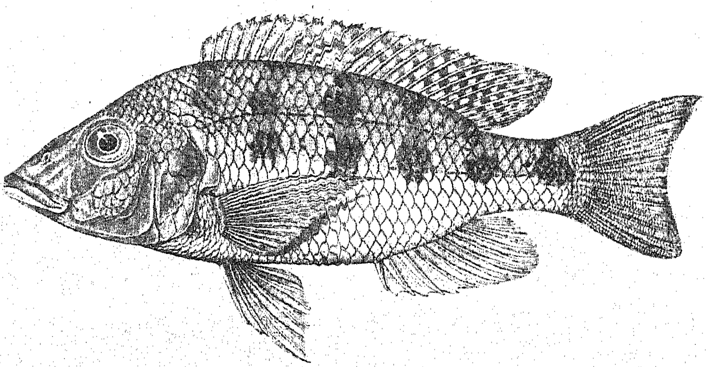
50. HAPLOCHROMIS MACRORHYNCHUS, sp. n. (Text-fig. 28.)

Tilapia rostrata (part.) Bouleng. Cat. Afr. Fish. iii. p. 255.

Depth of body $2\frac{2}{3}$ to $2\frac{3}{4}$ in length, length of head $2\frac{2}{3}$ to $2\frac{3}{4}$. Snout with straight or convex profile, longer than postorbital part of head. Diameter of eye 5 to $5\frac{1}{2}$ in length of head, interorbital width $3\frac{1}{4}$ to $3\frac{1}{2}$, depth of præorbital $3\frac{3}{4}$ to 4. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 4 or

5 series, outer bicuspid or posteriorly unicuspid, about 70 in outer series of upper jaw. 3 or 4 series of scales on cheek. Gill-rakers rather long, 15 to 17 on lower part of anterior arch. Pharyngeal teeth small. 34 or 35 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XV-XVI 11; last spine $\frac{1}{3}$ length of head. Anal III 9; third spine $\frac{1}{4}$ length of head. Pectoral $\frac{3}{4}$ length of head, nearly or quite reaching anal. Caudal emarginate. Caudal peduncle $1\frac{1}{3}$ to $1\frac{1}{2}$ as long as deep.

Text-figure 28.



Haplochromis macrorhynchus. $\frac{1}{2}$.

Upper half of body with 6 dark cross-bars broken up into 3 series of spots, the first of the lowest series on operculum, the sixth at base of caudal; dorsal with series of spots.

Three specimens, 190 to 210 mm. long (*d*, *Md*, *Moore*).

51. HAPLOCHROMIS ROSTRATUS Bouleng., 1899.

Tilapia rostrata (part.) Bouleng. Cat. Afr. Fish. iii. p. 255, fig. 172.

Depth of body $3\frac{1}{4}$ in length, length of head $2\frac{2}{3}$. Snout with convex profile, longer than postorbital part of head. Diameter of eye 4 in length of head, interorbital width $4\frac{1}{2}$, depth of præorbital $4\frac{1}{2}$. Jaws equal anteriorly; maxillary not extending to below eye; teeth in 3 well-separated series, outer bicuspid, 54 in outer series of upper jaw. 3 series of scales on cheek. Gill-rakers short, 19 or 20 on lower part of anterior arch. Pharyngeal teeth small. 34 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVI 12; last spine nearly $\frac{2}{5}$ length of head. Anal III 10; third spine $\frac{1}{3}$ length of head. Pectoral ? Caudal emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Colour nearly as in *H. macrorhynchus*, but the posterior bars more oblique and the fins unspotted.

The type, 105 mm. long.

52. HAPLOCHROMIS MACROSTOMA, sp. n. (Pl. IV. fig. 2.)

Depth of body 3 in length, length of head $2\frac{3}{4}$. Snout with profile a little concave in front of eye, thence straight, declivous, $2\frac{1}{2}$ as long as diameter of eye, which is $5\frac{1}{2}$ in length of head, less than præorbital depth, $\frac{2}{3}$ depth of cheek; interorbital width $4\frac{1}{2}$ in length of head. Jaws equal anteriorly; maxillary considerably exposed distally, extending to below anterior $\frac{1}{3}$ of eye; teeth small, conical, in 6 series. 6 series of scales on cheek. 12 gill-rakers on lower part of anterior arch. Pharyngeal teeth slender. 35 scales in a longitudinal series, 6 from origin of dorsal to lateral line. Dorsal XVI 10; last spine $\frac{2}{7}$, longest soft rays less than $\frac{1}{2}$ length of head. Anal III 10; third spine stronger than dorsals, $\frac{1}{4}$ head. Pectoral $\frac{2}{3}$ head, not quite reaching anal. Caudal very slightly emarginate Caudal peduncle $1\frac{1}{2}$ as long as deep. A series of about 8 dark spots on each side of back; a second series below lateral line, posteriorly confluent to form a band.

A single specimen, 260 mm. in total length (*Wood*).

11. LETHRINOPS, gen. n.
(type *Chromis lethrinus* Günth.).

Differs from *Haplochromis* in the dentition. Teeth very small and slender, in a few series, forming narrow bands which are interrupted at the symphyses; outer teeth mostly bicuspid, often unicuspid posteriorly, inner uni- or tri-cuspid.

Nyassa: four species.

Synopsis of the Species.

I. Pharyngeal teeth all small.

Snout shorter than postorbital part of head; maxillary not far short of vertical from anterior edge of eye .... 1. *albus*.
Snout longer than postorbital part of head; maxillary ending not far behind nostril .... 2. *macrorhynchus*.

II. Last few teeth of two middle series of lower pharyngeal somewhat enlarged.

10 gill-rakers on lower part of anterior arch .... 3. *lethrinus*.
12–13 gill-rakers on lower part of anterior arch .... 4. *leptodon*.

1. LETHRINOPS ALBUS, sp. n.

Tilapia macrophthalma (part.) Bouleng. Cat. Afr. Fish. iii. p. 261.

Depth of body equal to length of head, 3 in length of fish. Snout with straight profile, as long as diameter of eye, which is $3\frac{1}{4}$ in length of head, interorbital width 5, depth of præorbital $4\frac{1}{3}$. Jaws equal; maxillary not far short of vertical from anterior edge of eye; teeth in 2 series. 3 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 32 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 10. Anal III 9; third spine $\frac{2}{5}$ length of head, a little shorter than last dorsal. Pectoral as long as head, extending beyond origin of anal. Caudal scaly, emarginate. Caudal peduncle as long as deep. Silvery; an opercular spot.

A single specimen, 100 mm. in total length (*Whyte*).

2. LETHRINOPS MACRORHYNCHUS, sp. n.

Tilapia lethrinus (part.) Bouleng. Cat. Afr. Fish. iii. p. 254.

Depth of body $2\frac{1}{2}$ in length, length of head $2\frac{3}{4}$. Snout with straight profile, longer than postorbital part of head. Interorbital region flat. Diameter of eye $4\frac{1}{2}$ in length of head, interorbital width $4\frac{1}{2}$, depth of præorbital 3. Lower jaw projecting; maxillary ending not far behind nostril; teeth in 3 series. 3 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small. 33 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI 11; last spine $\frac{1}{3}$ length of head. Anal III 9; third spine less than $\frac{1}{3}$ head. Pectoral as long as head, extending nearly to middle of anal. Caudal scaly, emarginate. Caudal peduncle $1\frac{1}{3}$ as long as deep. A blackish band from nape along upper lateral line to base of caudal.

A single specimen, 180 mm. long (*Whyte*).

3. LETHRINOPS LETHRINUS Günth., 1893.

Tilapia lethrinus (part.) Bouleng. Cat. Afr. Fish. iii. p. 254, fig. 171.

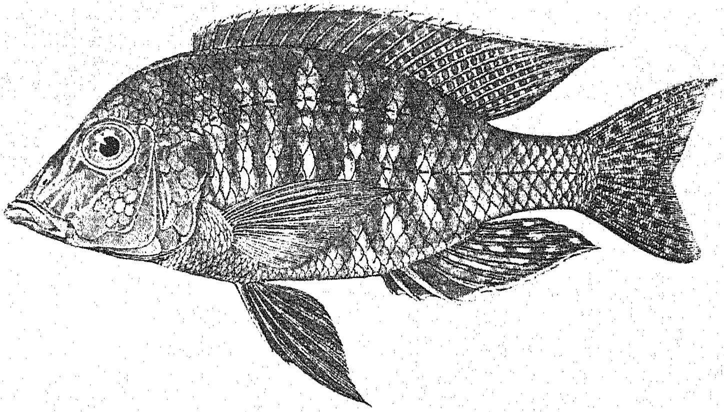
Depth of body $2\frac{1}{2}$ to $2\frac{3}{5}$ in length, length of head $2\frac{3}{4}$ to 3. Snout with straight profile, as long as postorbital part of head. Interorbital region flat. Diameter of eye $3\frac{3}{4}$ to $4\frac{1}{4}$ in length of head, interorbital width 4, præorbital depth 3 to $3\frac{1}{3}$. Lower jaw slightly projecting; maxillary extending to between nostril and eye; teeth in 3 to 5 series. 3 or 4 series of scales on cheek. 10 gill-rakers on lower part of anterior arch. Lower pharyngeal with the last few teeth of the two middle series a little enlarged. 32 to 34 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 11; last spine from less than $\frac{1}{2}$ to $\frac{3}{5}$ length of head. Anal III 9; third spine $\frac{1}{3}$ to $\frac{2}{5}$ head. Pectoral a little shorter than head, reaching origin of anal. Caudal densely scaled, emarginate. Caudal peduncle $1\frac{1}{3}$ to $1\frac{1}{2}$ as long as deep. A blackish lateral stripe running backwards above lower lateral line; sometimes a second above lateral line and a third near edge of back, or these may be represented by series of spots; dorsal spotted.

Three specimens, 140 to 200 mm. long (*Johnston, Moore*).

4. Lethrinops leptodon, sp. n. (Text-fig. 29.)

Depth of body 2⅖ to 3 in length, length of head 2⅘ to 3⅕. Snout with steep, straight or slightly convex profile, as long as or a little shorter than postorbital part of head. Interorbital region convex. Diameter of eye 3½ to 4 in length of head, interorbital width 3⅘ to 5, depth of præorbital 3 to 3½. Lower jaw slightly projecting; maxillary not extending to below eye; teeth in 3 or 4 series. 3 or 4 series of scales on cheek. 12 or 13 gill-rakers on lower part of anterior arch. Lower pharyngeal with the last few teeth of the two middle series a little enlarged. 31 to 34 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 10–13; last spine ⅖ to ½ length of head. Anal III 9-10; third spine ⅓ to ⅖ head. Pectoral nearly as long as head, reaching anal. Caudal scaly, emarginate. Caudal peduncle 1¼ to 1½ as long as deep. Silvery or bluish, with faint dark cross-bars; an opercular spot; an oblong dark blotch on lateral line below spinous dorsal, from just below which a dark band runs backwards to the caudal; dorsal and caudal with series of orange spots; dorsal sometimes with a yellow edge; anal with several ocelli in males.

Text-figure 29.



Lethrinops leptodon. ¾.

Eight specimens, 140 to 180 mm. in total length (*Wood*).

12. Docimodus Bouleng., 1896.

Differs from *Haplochromis* in the dentition. Teeth compressed, uni- or tri-cuspid, in 4 or 5 well-separated series; outer teeth large, forming a close-set series of about 20 in each jaw.

Nyassa; a single species.

DOCIMODUS JOHNSTONI Bouleng., 1896.

Docimodus johnstonii Bouleng. Cat. Afr. Fish. iii. p. 282, fig. 192.

Depth of body $2\frac{3}{4}$ to 3 in length, length of head 3 to $3\frac{1}{4}$. Snout convex, $1\frac{1}{4}$ to $1\frac{1}{2}$ diameter of eye, which is equal to or greater than depth of præorbital, 4 to $4\frac{1}{2}$ in length of head, interorbital width 3 to $3\frac{1}{2}$. Jaws strong; lower projecting; maxillary not extending to below eye. 3 or 4 series of scales on cheek. 10 or 11 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, compressed, bicuspid. 34 to 36 scales in a longitudinal series, 5 from origin of dorsal to lateral line. Dorsal XVI–XVII 9–11; last spine $\frac{1}{3}$ to $\frac{2}{5}$ length of head. Anal III 9–10; third spine as long as or a little shorter than dorsal. Pectoral as long as head, reaching anal. Caudal scaly, truncate, with slight median notch. Caudal peduncle $1\frac{1}{2}$ to $1\frac{3}{4}$ as long as deep. A dark lateral band from shoulder to base of caudal; a series of dark spots at base of dorsal; an opercular spot; dorsal with series of spots, in male with a dark intramarginal stripe and pale edge; anal and caudal, in the male, dusky with pale edge.

Four specimens, 160 to 250 mm. long (*Johnston*, *Wood*).

13. CYRTOCARA Boulenger, 1902
(type *C. moorii* Bouleng.).

Differs from *Haplochromis* in the structure of the spinous dorsal fin, which has the edge of the membrane straight between the tips of the spines. Teeth in several series, the outer enlarged, conical, or some bicuspid.

Nyassa.

Synopsis of the Species.

Jaws equal; caudal truncate or slightly emarginate …………………	1. *venusta*.
Jaws equal; caudal crescentically emarginate…………………………	2. *annectens*.
Lower jaw projecting ………………………………………………………	3. *moorii*.

1. CYRTOCARA VENUSTA.

Haplochromis venustus Bouleng. Cat. Afr. Fish. iii. p. 287, fig. 195.

Depth of body $2\frac{1}{2}$ to $2\frac{3}{4}$ in length, length of head 3 to $3\frac{1}{5}$. Snout with straight profile, as long as postorbital part of head. Diameter of eye $4\frac{1}{2}$ to 5 in length of head, equal to or a little less than præorbital depth; interorbital width $3\frac{1}{2}$ to 4 in length of head. Jaws equal anteriorly; maxillary not extending to below eye; teeth conical, or some of the outer bicuspid, in 4 or 5 series, outer larger. 3 or 4 series of scales on cheek. 11 or 12 gill-rakers on lower part of anterior arch. 32 to 34 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XV–XVI 10–11; last spine $\frac{2}{5}$ length of head. Anal III 10; third spine $\frac{1}{3}$ head. Pectoral as long as head, about reaching anal. Caudal scaly, truncate or slightly emarginate. Caudal peduncle 1⅕ to 1⅓ as long as deep. Bluish, with large vertically expanded blue-black spots tending to form irregular cross-bars; dorsal and anal with broad orange margin.

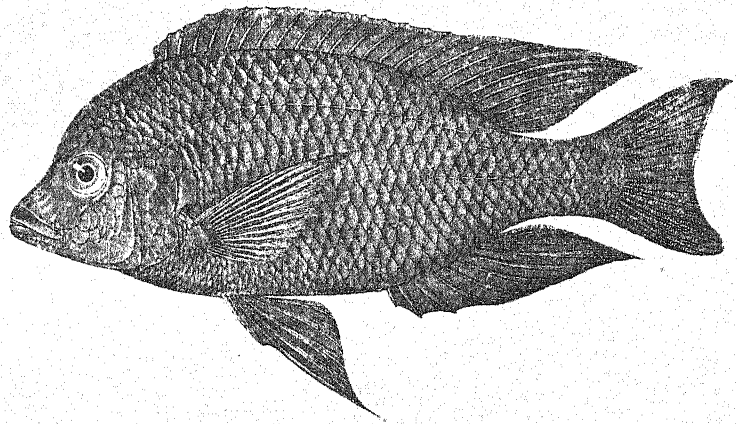
Four specimens, 170 to 200 mm. long (*Rhoades*).

Boulenger's figure shows a slight indication of lappets, but where the dorsal membrane is not torn its margin runs evenly between the tips of the spines.

2. CYRTOCARA ANNECTENS, sp. n. (Text-fig. 30.)

Depth of body 2⅓ to 2⅖ in length, length of head 3⅖ to 3½. Occiput convex, snout straight or slightly concave, a little shorter than postorbital part of head. Diameter of eye 4 to 4½ in length of head, equal to præorbital depth; interorbital width 3⅓ in length of head. Jaws equal anteriorly; maxillary not quite reaching to below eye; teeth conical, in 3 or 4 series, outer larger. 2 or 3 series of scales on cheek. 12 or 13 gill-rakers on lower part of anterior arch. 34 to 36 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVI–XVII 11–12; last spine ⅖ head. Anal III 8–9; third spine stronger and shorter than last dorsal. Pectoral as long as or a little longer than head, reaching anal. Caudal densely scaled, crescentically emarginate. Caudal peduncle 1⅓ to 1½ as long as deep. Uniformly bluish black.

Text-figure 30.



Cyrtocara annectens. ⅗.

Three specimens, 175 to 195 mm. in total length.

This species connects *C. venusta* with *C. moorii*, having the mouth formed as in the former, but in most other characters more nearly agreeing with the latter.

3. CYRTOCARA MOORII.

Very near the preceding species, but lower jaw projecting, some of the outer teeth pointing outwards, and maxillary extending to below eye. Occiput very convex. 3 or 4 series of scales on cheek. 11 gill-rakers on lower part of anterior arch. Dorsal XV–XVI 11. Anal III–IV 8–9.

14. RHAMPHOCHROMIS, gen. n.*

(type *Hemichromis longiceps* Günth.).

Form elongate. Snout produced, nearly or quite ½ length of head. Mouth with lateral cleft, ending far in front of eye; præmaxillaries with an anterior beak-like expansion; lower jaw deep; teeth conical, acute, biserial, or sometimes a third series anteriorly in upper jaw; teeth of outer series strong or moderately strong, set well apart; anterior teeth of second series in upper jaw enlarged. 16 to 18 gill-rakers on lower part of anterior arch. Scales 36 to 44. Dorsal XVI–XX 11–13; spines slender, rather short; soft fin rounded. Anal III 9–11; third spine about as long as and stronger than last dorsal. Pectoral rather short. Caudal scaly, emarginate.

Nyassa.

Synopsis of the Species.

I. Scales 36 to 40. Depth 4 to 4⅔ in length. Depth of caudal peduncle not less than half its length.

A. Interorbital width about 4 in head, diameter of eye 5½ to 6 (in specimens of 200 to 240 mm.); 3 or 4 series of scales on cheek.

Teeth moderate, 20 to 25 in outer series on each side .... 1. *longiceps.*
Teeth strong, 10 to 15 in outer series on each side .... 2. *ferox.*

B. Interorbital width about 5 in head; teeth strong.

Diameter of eye 5 in head (in specimens of 200 to 230 mm.); 3 or 4 series of scales on cheek................................. 3. *macrophthalmus.*
Diameter of eye 6 to 8 in head (in specimens of 160 to 330 mm.); 5 or 6 series of scales on cheek.................... 4. *woodi.*

II. Scales 43 or 44. Depth 4¾ to 5¼ in length.

Caudal peduncle 2¼ as long as deep; snout convex .... 5. *esox.*
Caudal peduncle 2¾ as long as deep; snout straight .... 6. *leptosoma.*

1. RHAMPHOCHROMIS LONGICEPS.

Hemichromis longiceps (part.) Günth. P. Z. S. 1864, p. 313.

Champsochromis longiceps (part.) Bouleng. Cat. Afr. Fish. iii. p. 434 (1915).

Depth of body 4 in length, length of head 2⅘. Diameter of eye 2½ in length of snout, 5½ in length of head; interorbital width 4 in length of head. Jaws meeting anteriorly; chin prominent; teeth moderate, 20 to 25 on each side in upper jaw. 4 series of scales on cheek. 36 to 38 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVII–XVIII 11–12; last spine $\frac{1}{4}$ length of head. Anal III 9. Pectoral $\frac{1}{2}$ length of head. Caudal peduncle $1\frac{2}{3}$ as long as deep. Silvery; back darker; an opercular spot.

---

* In the 'Zoological Record' for 1916, I named *C. cæruleus* as the type of *Champsochromis*; consequently a new name has to be found for the other species included in *Champsochromis* by Boulenger.

Description mainly based on a specimen 240 mm. long (*Moore*), which has been compared with one of the types, a skin of 220 mm. A skeleton has 36 (18+18) vertebræ.

2. Rhamphochromis ferox, sp. n.

? *Hemichromis longiceps* (part.) Günth. P. Z. S. 1864, p. 313.

Champsochromis longiceps (part.) Bouleng. Cat. Afr. Fish. iii. p. 434 (1915).

Depth of body 4 in length, length of head 3. Snout a little less than $\frac{1}{2}$ length of head. Diameter of eye 6 in length of head, interorbital width $4\frac{1}{4}$. Jaws meeting anteriorly; chin prominent; teeth strong, 10 to 15 on each side of upper jaw. 3 or 4 series of scales on cheek. 38 or 39 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XVII 12; last spine $\frac{1}{4}$ length of head. Anal III 10. Pectoral $\frac{1}{2}$ length of head. Caudal peduncle twice as long as deep. Silvery; back darker; an opercular spot.

Two spirit-specimens (*Moore*, *Rendall*), 200 and 240 mm. in total length. Günther's second type-specimen of *H. longiceps* probably belongs to this species.

3. Rhamphochromis macrophthalmus, sp. n. (Pl. VI. fig. 2.)

Depth of body 4 to $4\frac{1}{3}$ in length, length of head $2\frac{5}{6}$. Diameter of eye $2\frac{1}{4}$ in length of snout, 5 in length of head, equal to interorbital width. 3 or 4 series of scales on cheek. 38 to 40 scales in a longitudinal series, 5 to 7 from first dorsal spine to lateral line. Dorsal XVIII–XIX 11–12; last spine $\frac{1}{4}$ length of head. Anal III 10. Pectoral $\frac{3}{5}$ length of head. Caudal peduncle twice as long as deep. Silvery; back darker; a blackish opercular spot; dorsal and caudal greyish, pelvics and anal orange.

Three examples, 200 to 230 mm. in total length (*Wood*).

4. Rhamphochromis woodi, sp. n.

Champsochromis longiceps (part.) Bouleng. Cat. Afr. Fish. iii. p. 434, fig. 296 (1915).

Depth of body 4 to $4\frac{2}{3}$ in length, length of head $2\frac{2}{3}$ to $2\frac{3}{4}$. Snout $\frac{1}{2}$ length of head. Diameter of eye 6 to 8 in length of head, interorbital width $4\frac{3}{4}$ to 5. Lower jaw projecting. 5 or 6 series of scales on cheek. 38 to 40 scales in a longitudinal series, 6 or 7 from origin of dorsal to lateral line. Dorsal XVII–XIX 11–12; last spine $\frac{1}{5}$ to $\frac{1}{4}$ length of head. Anal III 10–11. Pectoral $\frac{3}{5}$ or a little less than $\frac{3}{5}$ length of head. Caudal peduncle

$1\frac{2}{3}$ to 2 as long as deep. Silvery, back darker; an opercular spot; soft dorsal and caudal spotted.

Four specimens, the one figured by Boulenger, 330 mm. long (*Rhoades*), and three of 160 to 215 mm. (*Wood*). A skeleton has 38 (18 + 20) vertebræ.

5. RHAMPHOCHROMIS ESOX.

Paratilapia esox (part.) Boulenger, Ann. & Mag. N. H. (8) ii. 1908, p. 240.

Champsochromis longiceps (part.) Boulenger, Cat. Afr. Fish. iii. p. 434 (1915).

Champsochromis esox (part.) Boulenger, *t. c.* p. 435, fig. 297.

Depth of body $4\frac{3}{4}$ in length, length of head 3. Snout with convex upper profile, $\frac{1}{2}$ length of head. Diameter of eye $7\frac{1}{2}$ to $8\frac{1}{2}$ in length of head, interorbital width $3\frac{3}{4}$. Lower jaw projecting; only the inner edge of præmaxillary sheathed by præorbital. 5 or 6 series of scales on cheek. 43 or 44 scales in a longitudinal series, 7 or 8 from origin of dorsal to lateral line. Dorsal XVIII–XX 12; last spine $\frac{1}{5}$ length of head. Anal III 10. Pectoral $\frac{1}{2}$ length of head. Caudal peduncle $2\frac{1}{4}$ as long as deep. Silvery; back darker; an opercular spot and a lateral band.

Two spirit-specimens, one of 370 mm. the type figured by Boulenger, the other 330 mm. long (*Moore*), and a skeleton with 39 (19 + 20) vertebræ.

6. RHAMPHOCHROMIS LEPTOSOMA, sp. n.

Paratilapia esox (part.) Bouleng. Ann. & Mag. N. H. (8) ii. 1908, p. 240.

Champsochromis esox (part.) Bouleng. Cat. Afr. Fish. iii. p. 435 (1915).

Depth of body $5\frac{1}{3}$ in length, length of head 3. Snout $\frac{1}{2}$ length of head, with straight upper profile; diameter of eye $7\frac{1}{2}$ in length of head, interorbital width 4. Distal half of præmaxillary sheathed by præorbital for nearly its whole width; jaws meeting anteriorly, but chin prominent. 6 series of scales on cheek. 43 scales in a longitudinal series, 7 from origin of dorsal to lateral line. Dorsal XIX 13; last spine $\frac{1}{6}$ length of head. Caudal peduncle $2\frac{3}{4}$ as long as deep. Silvery; back darker; a dark opercular spot and a lateral band.

A single specimen, one of the types of *P. esox*, 380 mm. in total length.

15. AULONOCARA, gen. n.

Frontal, nasal, orbital, præopercular, and mandibular bones with large channels with wide openings as *Trematocara*, from which *Aulonocara* may be distinguished externally by the bicuspid outer teeth, the more numerous dorsal spines, and the presence of two lateral lines.

Aulonocara nyassæ, sp. n. (Pl. V. fig. 1.)

Depth of body 2½ to 3 in length, length of head 2¾ to 3. Snout with straight or slightly convex profile, as long as post-orbital part of head. Diameter of eye 3⅓ to 3⅔ in length of head, equal to or greater than præorbital depth, greater than inter-orbital width. Jaws equal anteriorly; maxillary concealed, not extending to below eye; teeth small and slender, in 4 or 5 series, outer bicuspid, scarcely larger than inner. 9 or 10 gill-rakers on lower part of anterior arch. Pharyngeal teeth small, slender, bicuspid. 31 or 32 scales in a longitudinal series, 5 or 6 from origin of dorsal to lateral line. Dorsal XV–XVI 10–11; last spine ⅖ to ½ length of head. Anal III 9; third spine stronger and as long as or a little shorter than last dorsal. Pectoral as long as head, reaching anal. Caudal scaly, emarginate. Caudal peduncle longer than deep. Silvery; an opercular spot; about 10 faint dark cross-bars; dorsal with series of orange spots; lower fins orange (♀) or blackish, the anal with orange spots (♂).

Three specimens, 100–125 mm. long (*Wood*).

EXPLANATION OF THE PLATES.

Plate I.		*Haplochromis polystigma.*
Plate II.		,, *woodi.*
Plate III.		,, *præorbitalis.*
Plate IV.	fig. 1.	,, *eucinostomus.*
	fig. 2.	,, *macrostoma.*
Plate V.	fig. 1.	*Aulonocara nyassæ.*
	fig. 2.	*Haplochromis longipes.*
Plate VI.	fig. 1.	*Rhamphochromis macrophthalmus.*
	fig. 2.	*Haplochromis spilorhynchus.*

37. Note on the Systematic Position and Distribution of the Actinian *Sagartia luciæ*. By J. Playfair McMurrich, C.M.Z.S.

[Received September 19, 1921 : Read October 18, 1921.]

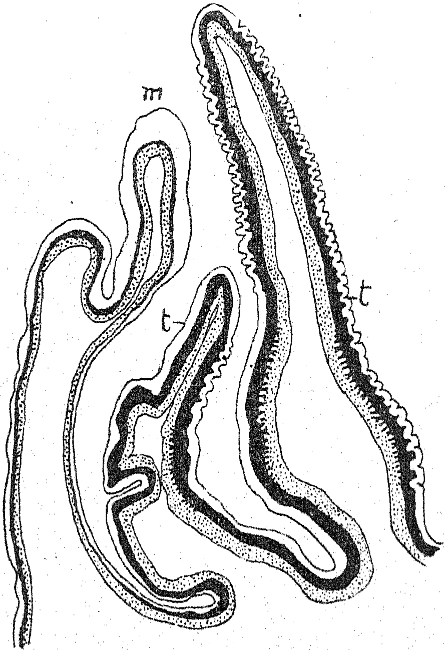
(Text-figures 1–4.)

During the last twenty years the small Actinian known as *Sagartia luciæ* has frequently been an object of study, and much is known as to its variations, methods of reproduction, powers of regeneration, reaction to light, locomotion, and general ecology. As yet, however, it has not been subjected to an anatomical investigation sufficiently detailed to reveal the features by which its systematic position may be determined.

It was first described in 1898 by Verrill, who gave a fairly full description of its external form and coloration, without, however, considering its anatomical structure. Later, Mrs. G. C. Davenport (1903) in a study of the variations in the number and arrangement of the vertical orange stripes, which are usually such a characteristic feature in the coloration of the column-wall, showed that reproduction by longitudinal division or by basal fragmentation was of frequent occurrence, variations in the number of the orange stripes resulting therefrom, as well as probably variations in the arrangement of the mesenteries, which, in the individuals with twelve stripes, were stated to be usually arranged in twenty-four pairs. But still there was lacking a sufficiently detailed account of the anatomy of the species to determine definitely its systematic affiliations, and other papers that have since dealt with it have not altered the situation in this respect. It may be well, therefore, to put on record some observations that were made several years ago, especially as they led to interesting conclusions not only as to the systematic position of the form, but also as to its distribution.

Concerning the disk and tentacles little need be said, further than to note the weakness of their musculature, the ectodermal fibres of the tentacles forming a simple layer on the smooth, or but slightly folded, surface of the mesoglœa; on the disk they may even be absent. Between the bases of the outermost tentacles and the apparent margin of the column there is a deep fosse, which is very characteristic of the species (text-fig. 1). It is evidently equivalent to the thin portion of the column-wall that intervenes in *Metridium senilis* between the outermost tentacles and the so-called collar, this latter being the upper edge of the strong mesoglœal sphincter. But whereas in *Metridium* this thin portion of the column is fully exposed in expansion, in *Sagartia luciæ* it remains introverted, thus producing the characteristic fosse. The mesoglœa forming its walls is very thin and smooth on both surfaces, and both the endoderm and ectoderm are also thin, the latter containing a few scattered and almost spherical mucous glands, without distinct indication of muscle fibres. The outer wall of the fosse joins the column proper at the apparent margin, and at once a change of structure is observable. The mesoglœa becomes decidedly thicker and its outer surface irregular; the ectoderm thickens and becomes richly supplied with gland cells, which, with the greater thickness of the layer, assume an oval or pyriform shape; and a weak circular endodermal musculature becomes evident. But there is no sign of a sphincter, either endodermal or mesoglœal. One would expect to find a mesoglœal sphincter just below the apparent margin, but in the several individuals that were sectioned I looked in vain for even traces of it.

Text-figure 1.

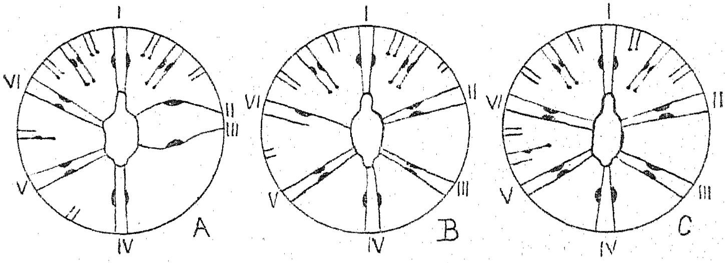


Sections through the margin and outermost tentacles of an individual from Woods Hole. *t*=tentacle; *m*=margin.

In two particulars, then, *Sagartia luciæ* differs notably from the typical members of the genus to which it has been assigned, namely, in the presence of a deep fosse and in the absence of a mesoglœal sphincter. In the one feature it shows some resemblance to *Metridium*, and in the absence of a sphincter it is paralleled by some members of the genus *Aiptasia*; neither of these genera, however, belonging to the same subfamily as *Sagartia*.

When one comes to consider the arrangement of the mesenteries, difficulties are at once encountered, because of the tendency of the species to reproduce by longitudinal fission. Some half-dozen individuals of which serial sections were prepared all showed irregularities in the arrangement of the mesenteries that may be reasonably attributed to this process, but nevertheless, they permit of inferences as to what the arrangement may have been before fission occurred. Three individuals may be taken as examples (text-fig. 2). In each of these in sections through the middle of the column there was a deep siphonoglyph at one end of the long axis of the stomodæum, and to this a pair of directive mesenteries with well-developed muscle pennons was attached. Opposite it was a second siphonoglyph which was relatively quite shallow, and to this a second pair of directives was attached, the muscle pennons of these being, however, very imperfectly developed. On either side of the fully-developed directives there were representatives of two cycles of imperfect mesenteries, and then came on either side a pair of perfect ones. So far the arrangement is quite regular except for the imperfect development of one siphonoglyph and its directives, but in two of the individuals, one member of each of the lateral pairs (II. and VI.) was decidedly less developed than the other. In these same two individuals (B and C) the pair II. is succeeded by another perfect pair (III.) poorly developed, and next this is the second pair of directives (IV.), no imperfect pairs occurring in the interspaces between II. and III. and III. and IV. Similarly, another pair of perfect mesenteries (V.) with fully-developed muscle pennons occurs between IV. and VI., and while no imperfect pairs occur in the interval between these and IV., in the interval on the other side there is in one individual a single small pair and in the

Text-figure 2.



Diagrams showing the arrangement of the mesenteries in three individuals from Woods Hole, Mass.

other two such pairs. These two individuals have, then, six pairs of perfect mesenteries and a number of imperfect ones disposed unsymmetrically. It is to be noted that this arrangement is that found in sections passing through the aboral half of the stomodæum; higher up, close to the bases of the tentacles, a number of additional rudimentary mesenteries may be found, but these need not be considered at present.

In the third individual (A) there were but five pairs of perfect mesenteries in sections passing through the aboral half of the stomodæum. Higher up, however, six occurred, with representatives of two cycles of imperfect ones in the intervals on either side of the fully-developed directives and in that between VI. and V., but only a single feeble pair in each of the other intervals. Following the series of sections aborally it is found that the change from the conditions showing six pairs of perfect mesenteries to that showing only five is due to the disappearance of a member of each of the pairs II. and III. together with the intervening imperfect mesenteries, the remaining members of the perfect pairs thus being brought into apposition and seeming to form a single pair.

The explanation which seems to fit these cases is that each is an example of an individual that has undergone longitudinal fission. The half of the body with the deep siphonoglyph and the representatives of three cycles of mesenteries shows the normal symmetrical arrangement characteristic of the species, and the irregularities and feeble development in the other half are indications of an attempt to regenerate the disturbed symmetry. It may be concluded that in the original individuals developed from ova there were three cycles of mesenteries arranged hexamerously, only those of the first cycle being perfect. The reproductive elements were not sufficiently developed in any of the individuals collected at Woods Hole to allow of a determination of their distribution, but in specimens collected at Plymouth it was found that they were limited to the pairs of the second and third cycles, *i.e.*, to the imperfect mesenteries. It may be added that both oral and marginal stomata occurred in the perfect mesenteries. Acontia are present, but are not abundant.

The structural features, then, that may be supposed to be characteristic of individuals that have not undergone fission are (1) the occurrence of a well-defined fosse; (2) the absence of a mesoglœal sphincter; (3) the occurrence of but six pairs of perfect mesenteries, which are also sterile, the reproductive elements being limited to the imperfect cycles. But before considering the significance of these features it will be well to consider the geographical distribution of the species.

Verrill's original description of *Sagartia luciæ* (1898) was based on individuals collected in Long Island Sound. He states that his attention was first directed to it in 1892 and expresses his conviction that it did not occur in any quantity in that region throughout the period 1865–1890. Furthermore it was stated to occur at Woods Hole in 1898, and Verrill collected there extensively during the period 1871–1887 without finding it. Parker (1902) added to these data observations on its occurrence at Newport in 1895 and at Nahant in 1899, it having been unknown in either of these localities before the dates mentioned, and he also records its occurrence at Salem, Mass., in 1901, that being apparently the northern limit of its distribution at that time. The records brought together by Parker seem to show clearly that the species has rapidly increased its distribution, at first eastward and then northward, until in ten years after it was first observed in Long Island Sound it had reached Salem. I have nothing to add to these records, except to state that in the summers of 1889 and 1890 I made special efforts to collect representatives of all the Actinian species occurring in the Woods Hole region and feel certain that, if *Sagartia luciæ* had occurred in that locality at that time in any considerable numbers, I could not have failed, as I did, to find it.

But whence did it come to Long Island Sound? Verrill suggests that it might have been brought from farther south on the shells of oysters that were annually brought north in large quantities and deposited in the waters of the Sound, and this possibility seems to find support in the following observations. In 1887 I described as *Sagartia pustulata* a form found on dead shells in shallow water in the vicinity of Beaufort, N.C. Its specific name was suggested by the appearance given to the column by the longitudinal and circular furrows that beset it, an appearance that may frequently be observed in living examples of *S. luciæ*, which form it also resembled in its coloration, except that the orange stripes of the column were lacking. This may seem an important difference, but undoubted individuals of *S. luciæ* without the characteristic stripes have been observed (Davenport, 1903; Walton, 1908). Unfortunately my preparations of *S. pustulata* are unsatisfactory and the preserved material has long since disappeared, so that I cannot determine the extent of its similarity to *S. luciæ*. This much, however, is certain, it has no sphincter; but there were only slight indications of the fosse, and it was not possible to determine the arrangement of the mesenteries. The points of resemblance shown by the two forms suggest their identity, but further observations are necessary to establish this and with it the extension of the distribution of the species so far to the south.

But the story of the distribution is far from being completed with the consideration of the west coast of the North Atlantic. Walton (1908) has placed on record the discovery at Plymouth in 1896 of a form which Mrs. Davenport later identified with *S. luciæ*. Previous to the date mentioned it had not been found in that locality, notwithstanding the extensive collections that had been made there, and from the Millbay Docks, where it was first observed, it has extended throughout the entire harbour and is now one of the common forms inhabiting the district. The evidence points to its being an introduced form, possibly from the other side of the Atlantic, but Walton suggests that neither New England nor South Devon was its original home, it having been introduced into both localities at approximately the same time.

There is another possibility, or rather a strong probability. In 1846 Mr. W. P. Cocks captured at St. Ives, on the north coast of Cornwall, a form which he later (1851) described as *Actinia chrysosplenium*. He sent drawings and a description of it to Johnston, who included it in his 'History of the British Zoophytes' (1847), and he conferred the same favour on P. H. Gosse, the drawing being this time the coloured one which is to be found reproduced in plate vi. of the 'Actinologia Britannica' (1860). Gosse referred it, with some doubts, to the genus *Sagartia* and added three additional localities at which it was found by Mr. Cocks, all on the Cornish coast, but neither he nor Johnston had personal knowledge of the form, their descriptions being based on notes furnished by Cocks.

Cocks's original figures do not suggest much resemblance to *S. luciæ*; they show relatively large circular spots scattered over the column, looking like verrucæ, but representing really, as may be gathered from the description, spots of bright yellow, the ground-colour varying "from a bright pea-green to the dark holly-leaf tint." But it is also stated that the yellow may be arranged in stripes instead of spots, and in the figure reproduced by Gosse it is so represented, the similarity to the coloration of *S. luciæ* being thus very great. In Gosse's figure, however, the tentacles are shown as if very few in number and plump; Cocks's original figure, on the other hand, represents them as much more numerous and tapering, quite as they are in *S. luciæ*. Combining the two figures, then, one would have a fairly accurate representation of a *S. luciæ*, both as regards its external form and its coloration. It is true that no acontia were observed; but *S. luciæ* is somewhat sluggish in emitting them, and the comparison that Cocks makes in a letter to Gosse of the appearance of the column-wall to that of a piece of "india-rubber when pierced with a pin" may well have been suggested by the somewhat pustulous appearance frequently presented by *S. luciæ*. Indeed, making allowances for the imperfections of descriptions of Actiniæ written before 1860, I do not hesitate to express the opinion that when examples of Cocks's species, taken in his localities, are studied, they will be found to be identical with *S. luciæ*.

If this opinion be correct then the species has been located on the southern coast of England at least since 1846, and its appearance at Plymouth in 1896 may have been merely an easterly extension of its area of distribution, similar to what occurred on the New England coast between 1891 and 1901. This would seem a simpler explanation of the facts than the supposition that it had been introduced from some distant locality.

I have sectioned a number of examples collected at Plymouth and find that they agree in all essential points with those from the New England coast. The irregularity of the mesenteries was somewhat more pronounced, one individual (text-fig. 3), for example, showing in sections through the aboral half of the stomodæum only two pairs of perfect mesenteries, situated opposite one another, one pair being directives attached to a well-developed siphonoglyph, while in the other pair the muscle pennons were on adjacent surfaces and there was no siphonoglyph. The members of this second pair, however, were attached to the stomodæum opposite the middle of its longer axis, and, although there were no mesenteries of younger cycles intervening, it seems probable that they represent members of two different pairs, II. and VI., there having been a failure of regeneration, after longitudinal fission, of the typical mesenteries. In the intervals between the directives and each of the other perfect mesenteries there were representatives of two other imperfect cycles, symmetrically arranged, those representing the second cycle bearing reproductive elements.

Text-figure 3.

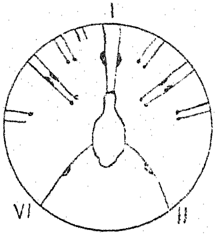
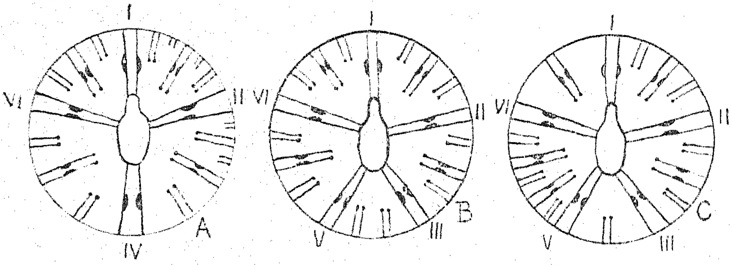


Diagram of the arrangement of the mesenteries in an individual from Plymouth.

Nor is the story of the distribution yet complete. In the summers of 1909 and 1911 I collected at the Canadian Biological Station at Departure Bay, on the east coast of Vancouver Island, an Actinian whose superficial resemblance to *S. luciæ* of New England was most striking, the only noticeable difference being a somewhat greater average size. They were of the same green colour, the column was adorned with the same characteristic longitudinal stripes of yellow or orange, and the tentacles showed the same form and coloration. They were found on Jesse Island, not far from the station, among the barnacles that closely covered the face of a large rock, in such a situation that for hours each day they were exposed by the tide. This was the only location in which they were observed in these years; but on a third visit to the station in 1912, I found them quite abundant in slight depressions and crevices in the sloping rocks forming the shore at the station, again well above low-water mark, so that they remained exposed to the air for several hours at each tide. I am confident that they did not occur on these rocks in the earlier years; had they then secured foothold upon them they could hardly have escaped observation. The rock on Jesse Island is not far from the station, but their extension to the latter locality is of interest in connection with the migrations of *S. luciæ* on the New England coast and at Plymouth. Many years ago Mr. Alexander Agassiz gave me a number of drawings of Actinians that he had collected in the Gulf of Georgia in 1859, and among these there were two that were unmistakably representations of the form under consideration. The drawings were made from specimens collected on Galliano Island, and furnish certain proof that the form has been in existence on the Canadian Pacific coast for over sixty years at least.

Text-figure 4.



Diagrams showing the arrangement of the mesenteries in three individuals from Departure Bay, British Columbia.

As has been stated, these Pacific forms resemble *S. luciæ* in their external form and coloration; their anatomical structure is also the same. They show a similar fosse, complete absence of a sphincter, and a similar arrangement of the mesenteries. The irregularities of the mesenteries were not so marked as in the Plymouth examples, but were nevertheless quite evident, as may be seen from the diagrams (text-fig. 4), which represent the arrangement observed in three individuals. In each case the individual was monoglyphic, with but a single pair of directives, and in one case there were only four pairs of perfect mesenteries, in the other two five pairs. Two cycles of imperfect and fertile mesenteries were present, in one case arranged symmetrically with regard to the four perfect pairs, but in the others showing some irregularity, and in the example with four pairs of perfect mesenteries representatives of a third imperfect cycle, without mesenterial filaments or reproductive elements, occurred in two of the interspaces. Acontia were present, but not abundant.

There can be no doubt as to the specific identity of the

Vancouver Island forms with those from New England and Plymouth, so that we now know of three areas inhabited by the species, separated from one another by wide intervals, two of them by the North Atlantic Ocean and the other from these by the whole width of the North American Continent. Furthermore, there is the certainty that the species has been "in residence" on the Canadian Pacific coast for over sixty years, and if the suggestion be correct that it has been secondarily introduced into the other two areas, the Pacific may have been its original home. But Mr. Cocks's discovery of his *A. chrysosplenium* on the Cornish coast dates back seventy-five years, and this lessens the probability of the introduction hypothesis. There is another possibility, however, namely, that originally the species had a circumpolar distribution, like *Metridium senilis*, *Urticina felina*, and a number of other Cœlenterate forms, and that its present areas of distribution are but separated remains of a much larger area. If further observations should reveal its presence on the Asiatic side of the Pacific the probability of this suggestion would be greatly increased*; in the meantime it is merely offered as an alternative to the introduction hypothesis.

But no matter what the original home of the species may have been, the evidence is clear that in each of its known localities it has in recent years more or less markedly extended its distribution. The cause of this is also obscure. It scores largely in favour of the introduction hypothesis, but is not necessarily a proof of it. It may be a phenomenon in some respects and on a lesser scale comparable to the migration of the Colorado Potato Beetle many years ago, but as to the influences that determine it in three widely separated areas I have no suggestion to make.

To return now to a consideration of the systematic affinities of the species. The possession of acontia marks it as a member of the family Sagartiadæ, a family in which several subdivisions are now recognized. From the subfamily Phellinæ it is excluded by the thinness of the column-wall and by the fact that acontia may be extruded through the wall, and it finds no place among the Sagartiinæ, since it has not more than six pairs of perfect mesenteries, these being also sterile. This leaves only the Metridiinæ and the Aiptasiinæ for its reception, and it is very doubtful if the separation of these two groups can be maintained. For the Aiptasiinæ differ from the Metridiinæ only negatively, in the lack of a mesoglœal sphincter, and since it may be supposed that they are descendants of forms possessing that structure, its absence in them is due to a process of reduction and is of less importance than the arrangement of the mesenteries. Furthermore, I have found in *Aiptasia* (*Heteractis*) *lucida* faint indications of a mesoglœal sphincter, and, I may add, since this observation has not been confirmed by others (Duerden, Pax) who have studied that species, that a quite distinct though feeble mesoglœal sphincter occurs in *A. pallida*. In the arrangement of the mesenteries the Aiptasias agree with the Metridiinæ, so that their separation from that subfamily seems to be artificial and unnecessary.

---

* Since possibilities are being discussed I may suggest that perhaps the form collected by Stimpson in Hong Kong Harbour and described by Verrill (1869) as *Sagartia lineata* may be the Asiatic representative of *S. luciæ*.

S. luciæ agrees with the majority of the Aiptasias in lacking a mesoglœal sphincter and in the possession of not more than six pairs of perfect mesenteries, and, with the Aiptasias, should be assigned to the subfamily Metridiinæ. That means that it is not entitled to the generic term *Sagartia*. When Gosse (1855) established the genus *Sagartia* he included in it all the forms known to him to possess acontia, with the exception of *Adamsia palliata*, which had already been assigned to a special genus by Forbes. In the list of the forms belonging to the new genus, Gosse placed *viduata* (*effœta*) first, and it might therefore be taken as the type species, but later, in the 'Actinologia Britannica' (1860), Gosse proposed the subdivision of *Sagartia* into a number of subgenera, retaining the original name for a group of forms of which *miniata* is the type, while *viduata* is referred with *troglodytes* (*undata*) and *parasitica* (*polypus*) to a subgenus *Cylista*. This complicates matters; for *miniata* and the other forms that Gosse associated with it are, apparently, referable to the older genus *Cereus*, and if this be the case *Sagartia* becomes merely a synonym, unless *viduata* (*effœta*) be accepted as its type species. This seems the proper thing to do, for otherwise the confusion that now exists in Actinian nomenclature would become still worse confounded.

Sagartia viduata, or, to give it its more correct name, *S. effœta* L., has no fosse and a well-developed mesoglœal sphincter; my preparations from specimens collected at Plymouth do not allow of certainty as to the arrangement of the mesenteries, though the indications were that more than six pairs were perfect, but Carlgren (1893) has shown that this is the case. *Sagartia*, then, as is seemly, belongs to the subfamily Sagartiinæ, and our *S. luciæ* cannot be referred to it. What, then, is the proper generic term for this species? It has some resemblance to *Aiptasia*, but, lacking the characteristic double row of permanent cinclides of that genus, it cannot well be included in it. It has already been pointed out that there is a strong probability, indeed, I believe it is more than a probability, that it is identical with the *A. chrysosplenium* of Cocks, and that form Gosse recognized as a *Sagartia*, referring it to a special subgenus *Chrysoela*. If my belief as to its identity is well founded, *S. luciæ* should be known as *Chrysoela chrysosplenium* (Cocks) Gosse. At all events it is not a *Sagartia*, nor can it be assigned to any of the genera now recognized.

BIBLIOGRAPHY.

1847. JOHNSTON, G.—A History of the British Zoophytes. London.

1851. COCKS, W. P.—Actiniæ procured at Falmouth and its neighbourhood. Report Roy. Cornwall Polytech. Soc. xix.

1855. GOSSE, P. H.—Description of *Peachia hastata*, a new genus and species of the class Zoophyta, with observations on tha family Actiniadæ. Trans. Linnean Soc. xxi.

1860. GOSSE, P. H.—Actinologia Britannica. London.

1869. VERRILL, A. E.—Synopsis of the Polyps and Corals of the North Pacific Exploring Expedition, etc. Proc. Essex Inst. vi.

1887. MCMURRICH, J. P.—Notes on Actiniæ obtained at Beaufort, N.C. Studies from Biol. Lab. Johns Hopkins Univ. iv.

1893. CARLGREN, O.—Studien über nordische Actinien—I. Kgl. Svensk. Vetensk. Akad. Handl. xxv.

1898. VERRILL, A. E.—Descriptions of new American Actinians, with critical notes on other Species—I. Amer. Journ. Sci. ser. 4, vi.

1900. PARKER, G. H.—Synopses of North American Invertebrates—XIII. The Actinians. American Naturalist, xxxiv.

1902. PARKER, G. H.—Notes on the dispersal of *Sagartia luciæ*, Verrill. American Naturalist, xxxvi.

1902. HAZEN, ANNA P.—The Regeneration of an Œsophagus in the Anemone, *Sagartia luciæ*. Archiv f. Entwicklungsmech. der Organismen, xiv.

1903. HAZEN, ANNA P.—Regeneration in the Anemone, *Sagartia luciæ*. Archiv f. Entwicklungsmech. der Organismen, xvi.

1903. DAVENPORT, GERTRUDE C.—Variation in the number of stripes on the Sea-Anemone, *Sagartia luciæ*. The Mark Anniversary Volume.

1907. HARGITT, C. W.—Notes on the Behaviour of Sea-Anemones. Biol. Bulletin, xii.

1908. WALTON, C. L.—Notes on some Sagartiadæ and Zoanthidæ from Plymouth. Journ. Marine Biol. Association, N.S., viii.

1917. PARKER, G. H.—Pedal Locomotion in Actinians. Journ. Exp. Zool. xxii.

1919. D. W. DAVIS.—Asexual multiplication and regeneration in *Sagartia luciæ* Verrill. Journ. Exp. Zool. xxviii.

1919. HAUSMAN, L. A.—The Orange-striped Anemone (*Sagartia luçiæ* Verrill). An Ecological Study. Biol. Bulletin, xxxvii.

38. The Comparative Anatomy of the Tongues of the Mammalia.—V. Lemuroidea and Tarsioidea. By CHARLES F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

[Received August 8, 1921: Read November 8, 1921.]

(Text-figures 66–69.)

CONTENTS.

	Page
Introduction	741
The Sublingua	741
The Lytta	742
Family Lemuridæ	742
,, Indrisidæ	746
,, Lorisidæ	747
,, Galagidæ	750
,, Chiromyidæ	751
,, Tarsiidæ	753
Summary and Conclusions	753
Bibliography	754

INTRODUCTION.

The literature of the tongues of the Lemuroidea and Tarsioidea is extensive, but it deals mainly with the organs of taste and the characters and significance of the sublingua. A few tongues have been described in detail in monographs on certain animals*, but little attention has been paid to some features which are of value for purposes of classification. The present paper is based on the examination of specimens in the Society's Prosectorium and the Museum of the Royal College of Surgeons, the latter being described as Mus. R.C.S.

In the Lemuroidea and Tarsioidea the foramen cæcum and apical gland of Nuhn are absent. Some have no lateral organs, and the lytta appears for the first time in the Primates. The frenal lamellæ are sometimes very complex.

The Sublingua.

The first description was contained in Tiedemann's paper on *Stenops* (**18**), but John Hunter had observed it previously and likened it to the tongue of a bird. It is horny, devoid of taste buds, and fixed to the mandible by a frenum. Small muscle bundles derived from the hyoglossus and genioglossus run into it.

It is lyrate (Lemuridæ and Indrisidæ) or tongue-shaped (Lorisidæ and Galagidæ), and has a variable number of apical denticles which differ in character in different animals; these are absent in *Tarsius* and *Chiromys*, but the latter has a strong projection on the centre of its anterior border.

---

* See papers 2, 3, 6, 7, 13, 14, and 16 in Bibliography.

Crests are present on the ventral surface in all species. They are three in number in the Indrisidæ and Lemuridæ, except *Microcebus*, but only one is present in the Lorisidæ, Galagidæ, *Microcebus*, *Chiromys*, and *Tarsius*. The dorsal surface bears a crest of variable size in the Lorisidæ and Galagidæ, the most pronounced one occurring in *Perodicticus potto*.

The consistence varies greatly. In all the Lemuroidea the sublingua is horny, but in *Tarsius* it is soft. In the Lemuridæ and Indrisidæ the entire sublingua is uniformly thick, but in the Lorisidæ, Galagidæ, and *Chiromys* the central parts are thicker and harder than the lateral parts. The horny covering is produced by an excessive thickening of the stratum corneum.

In *Lemur* the sublingua can be separated to a considerable extent from the under surface of the tongue, but in *Tarsius* they cannot be separated, for the sublingua is demarcated from the tongue by a slight groove only. In the Lorisidæ and Galagidæ the degree of mobility is intermediate, and in *Chiromys* it is greater than that described in the writings of Gegenbaur (**5**) and Pocock (**15**).

I have already summarised the differences between the sublinguæ of the Prosimiæ and Marsupialia (**20**).

Flower (**4**) and Pocock (**15**) believe that the function of the sublingua is to clean the posterior surfaces of the incisor teeth; but others think it has no function, and regard it purely from the point of view of phylogeny. I believe that the sublingua of the Marsupialia is entirely a vestigial structure.

The Lytta.

The tongues of the Lemuroidea and Tarsioidea have lyttæ which are of two kinds:—1. The lytta of the tongue. 2. The lytta of the sublingua.

The lytta of the sublingua is absent in *Lemur*, double in *Tarsius*, and single in *Perodicticus* and *Loris*; in all these forms it is internal, but in *Chiromys* it forms a strong, external, nodulated ridge ending anteriorly in a hook.

The lytta of the tongue is present in *Perodicticus*, *Loris*, and *Chiromys*, but Gegenbaur and Owen missed it in the latter. It is connected to the lytta of the sublingua by connective tissue.

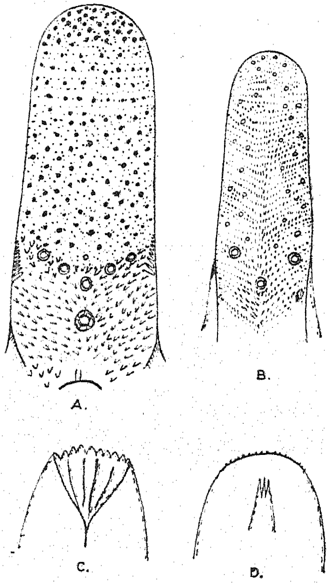
I have nothing to add to existing accounts of the histology of the sublingua and lytta.

Family LEMURIDÆ.

Genus LEMUR.

In all species the apex is rounded and covered with small conical and fungiform papillæ, but has no notch. The lateral borders increase in thickness from before backwards and have lateral organs at their posterior extremities. The oral part of the dorsum possesses several wide, shallow transverse ridges and sulci, and there is a smooth, non-papillary area in front of the epiglottis bisected by the median glosso-epiglottic fold. Small ridges may be present under the apex and send forward pointed processes (text-fig. 66 C).

Text-figure 66.



The tongues of *Lemur catta* (A) and *Nycticebus tardigradus* (B); C and D, the under surfaces of two examples of the tongue of *Lemur rufifrons*.

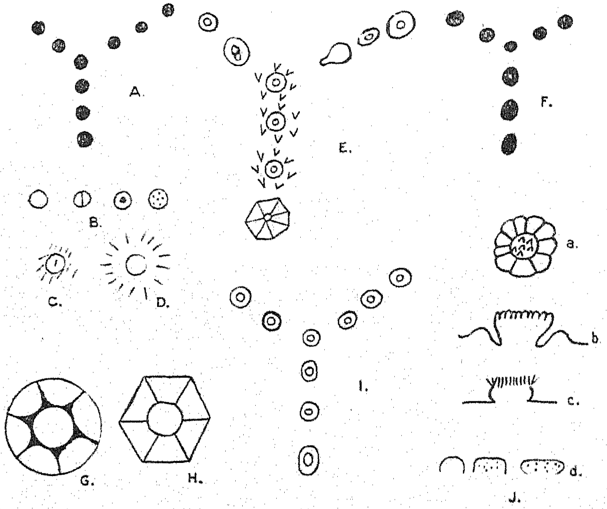
The circumvallate papillæ are arranged in Y-formation in most species. They are round or oval, and are surrounded by an annular or lobulated vallum. They may be equal in size, or the most posterior papilla may be the largest. The following arrangements were seen by me or recorded by others:—

1. *Lemur catta*: Six papillæ in Y-formation (text-fig. 66 A).
2. *L. fulvus*: Nine papillæ in Y-formation (text-fig. 67 A).
3. *L. fulvus rufifrons*: Nine papillæ in Y-formation (text-fig. 67 E).
4. *L. macaco*: Eight papillæ in Y-formation (text-fig. 67 F).
5. *L. varius*: Five papillæ in Y-formation.
6. *L. mongoz*: Nine papillæ in Y-formation (text-fig. 67 I).
7. *L. mongoz*: Four papillæ forming a double pair.
8. *L. melanocephala*: Nine papillæ in Y-formation (Münch).
9. *L. rubriventer*: A pair of papillæ (Münch).

The papillæ may be concealed by the long conical papillæ on the base of the tongue (text-fig. 67 C), or there may be a clear zone between them (text-fig. 67 D).

The fungiform papillæ, which are small and numerous, stretch right across the dorsum, but have the usual arrangement in clusters and rows. The transverse ridges extend far forwards at the expense of the apical cluster. On the ventral papillary zone they are scanty and only form a single row.

Text-figure 67.

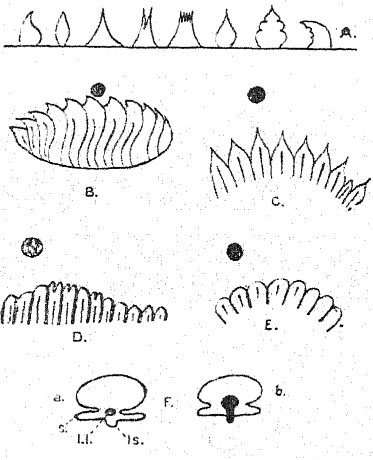


The vallate papillæ of the Lemuroidea: A–D. *Lemur fulvus*; E. *L. rufifrons*; F–H. *L. macaco*; I. *L. mongoz*; Ja–Jc. plan and elevation of papillæ of *L. rubriventer*; Jd. fungiform papillæ of *Lemur*.

The conical papillæ (text-fig. 68 A) have the usual arrangements in clusters and rows, and their points run in the usual directions. Those on the oral part of the dorsum are small, but those on the pharyngeal part are big and cylindrical or scale-like. These two groups are separated by a line of demarcation concave forwards, lying a little in front of the vallate papillary area. The points of the basal papillæ are straight or recurved. This arrangement is also present in *Hapalemur*, according to Beddard (1), and *Chiromys*, but is absent in *Microcebus*, the Lorisidæ, Galagidæ, and *Tarsius*.

The lateral organs (text-fig. 68 B–E) consist of laminæ and sulci on the dorsum alone (*L. macaco*) or on the lateral borders and inferior surface. The central laminæ are larger than the lateral ones, and the inner border of each organ is convex towards the lateral vallate papillæ as in the Simiidæ. The relative position of these papillæ to the organs varies in different species, lying level with the central or posterior laminæ. In *Microcebus* the lateral organs are absent, and this condition, together with the number and arrangement of the vallate papillæ and state of the conical papillæ, links the tongue to those of the Lorisidæ and Galagidæ and distinguishes it from those of *Lemur*. The numbers of laminæ and sulci frequently differ in the two organs of the same tongue, and the secondary sulci may be well marked or indistinct.

Text-figure 68.



A. Conical papillæ of *Lemur*; B–E. lateral organs of *L. catta* (B), *L. fulvus* (C), *L. macaco* (D), *L. mongoz* (E); F. cross sections of the tongue of *Chiromys* in the anterior (a) and middle (b) thirds: (s. sublingua, l.l. lytta of tongue, l.s. lytta of sublingua).

The ventral papillary zone is narrow and has many conical but few fungiform papillæ, and the ventral mesial sulcus may contain a mesial crest; it is absent altogether in some examples of each species, but present in others.

The sublingua (text-fig. 69) is triangular or lyrate, and the apex is divided into a small group of slender denticles. The edges are serrated in *L. catta*, *L. macaco*, and *L. varius*, and entire in *L. fulvus* and *L. fulvus rufifrons*. The median crest is well developed, but the lateral ventral crests vary in size. Between the base of the sublingua and the frenal lamellæ is a deep sulcus which is sometimes **V**-shaped.

The frenum consists of two lax portions separated by the sublingua. The first extends from the floor of the mouth to the under surface of the sublingua, and the second runs from the upper surface of the sublingua to the mesial ventral sulcus of the tongue. The frenal lamellæ, which are sometimes complex, have the following characters:—

1. *L. catta*: lamellæ are two blunt rounded processes.
2. *L. coronatus*: lamellæ form a parallel-sided flap.
3. *L. macaco*: triangular with rounded apex and lobulated sides.
4. *L. varius*: two broad flaps with rounded anterior borders and sharply cut mesial borders.
5. *L. mongoz*: lamellæ form a parallel-sided flap.

The tongues of the species of *Lemur* resemble those of the Chimpanzee and Gibbons in the following respects:—

1. Several vallate papillæ form a **Y**.
2. The conical papillæ on the pharyngeal part of the tongue are much larger than those on the oral part.
3. The lateral organs are situated at the posterior parts of the lateral borders and are convex towards the lateral vallate papillæ.

The tongues differ from those of the Orang-Outan and Man, which have no large conical papillæ on the pharyngeal part of the tongue, and the vallate papillæ form a **V**. These also have the Apical Gland of Nuhn.

They differ from those of the Gorilla and Orang-Outan, whose lateral organs form ladder-like patterns on the dorsum.

Genus MICROCEBUS.

SMITH'S DWARF LEMUR (*M. murinus*).

Three vallate papillæ form a triangle with the base anterior; the basal papillæ are small and circular, but the apical papilla is large, round, and granular.

The conical papillæ increase in size from the apex of the tongue to the epiglottis, and those on the base are not disproportionately large as in *Lemur* and *Hapalemur*.

Lateral organs are absent.

The sublingua is a flat horny plate with a row of denticles on its anterior border.

One can see, therefore, that there is no resemblance in any of the essential points between the tongues of *Lemur* and *Microcebus*, but the latter resemble those of some of the Lorises, Galagos, and Pottos, described below.

Family INDRISIDÆ.

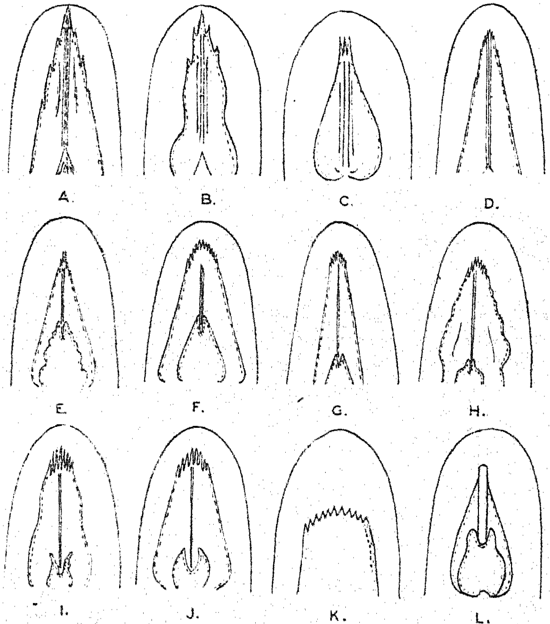
Genus INDRIS.

Flower (4) described the tongue of *I. brevicaudatus* as follows:—"The tongue is long and narrow, with an obtuse point at the apex, being less truncated than in *Lemur*. It is

$2\frac{1}{2}$ inches long, and $\frac{7}{8}$ inch broad at its widest point. The dorsal surface is covered with a very close-set velvety pile of small papillæ, apparently all of one kind. There are two small circumvallate papillæ, $\frac{3}{10}$ inch apart, just in front of the attachments of the palato-glossal folds."

The sublinguæ resemble those of the Lemuridæ.

Text-figure 69.



The sublingua of *Lemur catta* (A.B), *L. fulvus* (C), *L. rufifrons* (D), *L. macaco* (E); *Nycticebus tardigradus* (F.G); *Loris gracilis* (H); *Perodicticus potto* (I); *Hemigalago demidoffi* (J); *Galago crassicaudata* (K); *Tarsius spectrum* (L).

Family LORISIDÆ.

Genus NYCTICEBUS.

THE SLOW LORIS (*N. tardigradus*).

Three preserved specimens were examined, and their lateral borders were seen to have no lateral organs. The apex, sulci, and bare area in front of the epiglottis were similar to those of *Lemur*.

Three vallate papillæ (text-fig. 66 B) form an equilateral triangle with the base behind. All are circular, prominent, and finely granular; the fossæ are well marked and the vallums appear as clear zones. They are conical on elevation, the bases of the cones projecting beyond the fossæ. In two specimens the papillæ are of equal size, but in the third (Mus. R.C.S.) the apical papilla is smaller than the basal ones.

The fungiform papillæ are not numerous, and form a dorsal bounding zone on which they have the usual arrangement in rows and clusters, but the apical cluster is small; and they are few in number on the ventral papillary zone.

The conical papillæ have the usual arrangement in clusters and rows; they increase in size from apex to epiglottis, and there is no sharp transition between small conical papillæ on the oral and large papillæ on the pharyngeal part of the dorsum as in *Lemur* and *Hapalemur*.

Lateral organs are absent.

The sublingua differed in two of my specimens. In the first it is tongue-shaped with a broad base whose angles are rounded, and its area is half that of the inferior surface of the tongue. The denticles on the centre of the anterior border are large, but the more lateral ones are smaller. The central part of the sublingua is thick and strong, but the lateral parts are thin. On the ventral surface there is only one strong median ridge, and the upper surface has a strong ridge which is received into the median ventral sulcus of the tongue. The frenum is long and lax, so the sublingua is freely movable. In my second specimen the sublingua has no rounded basal angles, the apical denticles are more closely packed, there is only a faint ridge on the upper surface, and the whole organ is more fixed to the under surface of the tongue.

The frenal lamellæ of the first specimen are broad, with bluntly rounded apices, but they are narrow and pointed in the second example. Supplementary lamellæ were present in Pocock's specimen (**15**).

The median ventral sulcus has no crest, but receives the ridge on the upper surface of the sublingua.

Genus Loris.

The Slender Loris (*Loris gracilis*).

The conical tongue narrows rapidly from base to apex, and its proportions are small.

Three vallate papillæ form an isosceles triangle with the apex behind. All are circular, furrowed, and granular, and are surrounded by prominent vallums. None are overlapped by conical papillæ.

The fungiform papillæ differ from those of *Nycticebus tardigradus* in that they extend right across the dorsum. They have the usual arrangement in rows and clusters, but the transverse rows extend far forwards at the expense of the apical cluster. Those at the posterior part of the oral division of the dorsum are large, hemispherical, polished, and close together. Few are present on the inferior surface of the tongue.

The conical papillæ resemble those of *Nycticebus tardigradus* in their mode of enlargement from before backwards, and differ from those of *Lemur* and *Hapalemur*. Most of the papillæ are cylindrical, and are surrounded by zones of interpapillary dorsum.

Lateral organs are absent.

The following account of the sublingua (text-fig. 69) is supplementary to those of Tiedemann (**18**), Otto, Vrolik (**16**), and Gegenbaur (**5**). It is leaf-shaped and wrapped round the convex inferior surface of the tongue, so it is concavo-convex on cross section. The edges are finely crenated and the apex is sharp. The denticles are smaller, less numerous, and more closely packed than those of *Nycticebus tardigradus*, but the characters of the central and lateral parts are similar in both cases. The mesial dorsal crest is not so pronounced as that of some examples of *Nycticebus*, but is equal to that of others. Both species have equally mobile sublinguæ, but the freedom is less than that of *Lemur*.

The frenal lamellæ are two small, rounded processes whose edges extend postero-laterally for a considerable distance. No accessory lamellæ are present.

The median ventral sulcus resembles that of *Nycticebus tardigradus*.

Genus PERODICTICUS.

BOSMAN'S POTTO (*Perodicticus potto*).

The tongue, which narrows slightly from base to apex, has no apical notch and no mesial dorsal sulcus, but possesses a few small, narrow transverse sulci in the posterior part of the oral division of the dorsum.

The circumvallate papillæ.—Van der Hoeven (**6**) described and figured three large papillæ in a triangle with the apex behind. In the specimen in the Museum of the Royal College of Surgeons there are three large excavated papillæ forming a triangle. In my specimen there are three in a triangle, but the apical papilla is divided into two large elongated parts enclosed in the one fossa.

The fungiform and conical papillæ do not differ materially from those of *Nycticebus tardigradus*.

Lateral organs are absent.

The sublingua is tongue-shaped and has nine apical denticles as in *P. ibeanus*. Its strong median ventral crest is bifurcated posteriorly, and the dorsal ridge is larger and sharper than that of any other species which I examined. The edges are devoid of serrations and the degree of mobility is equal to that which exists in *Nycticebus* and *Loris* (text-fig. 69).

Nussbaum (**11**) pointed out that the sublingua has a rod-like core, which he termed the "lyssa of the sublingua." It has a connective-tissue sheath and consists of fat, cartilage, and connective tissue. It is connected above to the lyssa of the tongue which contains fat, connective tissue, and muscle fibres.

The frenal lamellæ are two conical processes whose crenated edges extend postero-laterally almost as far as the palato-glossal folds.

The median ventral sulcus has no crest, but receives the prominent median dorsal ridge on the sublingua.

Family GALAGIDÆ.

Genus GALAGO.

THE BUSHY-TAILED GALAGO (*G. crassicaudata*). Mus. R.C.S.

The tongue was preserved, so no measurements were made.

Three vallate papillæ are arranged in the form of an isosceles triangle with long sides. They are large, oval, and excavated, the fossæ are patulous, and the vallums appear as clear zones. The basal pair are opposite the attachments of the palato-glossal folds. Flower (4) also recorded three papillæ in the form of a triangle.

The fungiform papillæ are small, rounded, and arranged in the usual manner.

The conical papillæ increase in size from before-backwards, and there is no sharp line of contrast between those on the oral and those on the pharyngeal parts of the tongue as in *Lemur* and *Hapalemur*. Flower states that they are thick on the base of the tongue. They have denticulated points directed backwards.

The lateral organs are absent, the mesial ventral sulcus has no crest, and the ventral papillary zone has no fungiform papillæ.

The sublingua (text-fig. 69), which is flat, horny, and tongue-shaped, has a rounded anterior border bearing sixteen squat sharp-pointed denticles. It covers rather more than half of the width of the under surface of the tongue and half of the length of the free part between the apex and frenum. The sides are parallel and entire. Flower's specimen had upturned edges and a downwardly-directed apex which adapted its form to that of the under surface of the tongue.

Genus HEMIGALAGO.

DEMIDOFF'S HEMIGALAGO (*H. demidoffi*).

The small conical tongues of both my specimens have three vallate papillæ arranged in the form of a triangle with the apex directed backwards; the basal papillæ are small and circular, and the apical papilla is large, circular, and granular, with a patulous fossa.

The fungiform papillæ are not numerous, but stand up prominently. They have the usual arrangement, but the apical cluster is small. They form a well-marked row of closely-set elements on the posterior third of each lateral border of the tongue. None are present on the inferior surface of the tongue.

The conical papillæ give the surface of the tongue a finely-granular appearance. They increase in size from before backwards, and there is no sharp contrast between the papillæ on the oral and pharyngeal parts of the tongue as in *Lemur* and *Hapalemur*. When the tongue is dried they stand up prominently and reach a higher level than the summits of the fungiform papillæ. They form a narrow ventral papillary zone.

Lateral organs are absent.

The sublingua (text-fig. 69), which is flat, horny, and tongue-shaped, has a rounded, denticulated, comb-like anterior border, and nearly parallel, entire edges. It has a well-marked median crest, but no lateral ridges, and it covers a larger area of the under surface of the tongue than that of the *Galago*.

The frenal lamellæ are small and pointed, and the mesial ventral sulcus does not contain a crest.

Pocock (**15**) described nine apical denticles on the sublingua of *Galago monteiri*.

Family CHIROMYIDÆ.

Genus CHIROMYS.

THE AYE-AYE (*C. madagascariensis*).

The following description is supplementary to the existing accounts by Owen (**13**) and Peters (**14**):—

Measurements.—Total length 4·6 cm.; oral part 3·1 cm.; pharyngeal part ·5 cm.; width between the lingual attachments of the palato-glossal folds 1·6 cm.

The apex is thick and rounded, but has no notch, and the massive lateral borders are devoid of lateral organs. Mesial dorsal and mesial ventral sulci are absent.

Three circumvallate papillæ are arranged in the form of a triangle with the apex behind. All are circular and granular, and surrounded by nodulated vallums. Owen described two papillæ, about two lines apart, lying about an inch and a half behind the apex of the tongue. Peters recorded three papillæ arranged in a triangle, and figured nodulated vallums.

The fungiform papillæ are not numerous. They extend right across the dorsum, but are scanty in the middle line. They have the usual arrangement, but the apical dorsal cluster is small. One large papilla bisects the base of the vallate papillary triangle.

None are present on the inferior surface of the tongue. They are smooth or granular, and are hemispherical or pedunculated.

The conical papillæ have the usual arrangement. They are closely packed and exhibit considerable mutual compression. Some are low and cylindrical, but others stand up prominently.

The papillæ on the oral part of the tongue are smaller than those on the base, and a line of demarcation, concave forwards, separates the two groups. The tongue resembles those of *Lemur* and *Hapalemur* in this respect, and differs from those of the Lorises, Pottos, and Galagos. There is also an area devoid of papillæ in front of the epiglottis; this is bisected by the median glosso-epiglottic fold.

The sublingua has been described by Owen (**13**), Gegenbaur (**5**), and Pocock (**15**), but several details are omitted, or not sufficiently emphasised, in their accounts.

It is a flat horny plate with entire lateral margins and a rounded anterior border with a central projection, whose point marks the place where the strong, denticulated median ventral ridge bends downwards in a hook. This crest increases in depth from behind-forwards, and its hook lies 9 mm. posterior to the apex of the tongue.

It was shown in the descriptions of the sublinguæ of the Lorises that there is a thick central strip and two thin lateral parts. The same parts are present in *Chiromys*, but differ from those of the Lorises in that the central part is adherent to the under surface of the tongue, but the lateral parts are free; in the Lorises, on the other hand, both parts are free. Gegenbaur and Pocock both describe a free lateral margin, but do not give any idea of the extent of the free part. In my specimen the total width of the sublingua is 1·2 cm.; the central firm adherent part is ·6 cm. wide, and each free lateral part is ·3 cm. wide. A probe can be passed for a considerable distance between the under surface of the tongue and the sublingua. No denticles project from the anterior border.

Pocock (**15**) described the two small glandular (?) pockets on each side of the frenum, and pointed out that the frenal lamellæ are narrow.

Gegenbaur (**5**) described the horny nature of the sublingua, but did not show how the thickness varies in different parts. Although one thinks that the central parts are thicker than the lateral parts, when the tongue is entire, one sees that the reverse is the case when sections are made. The apparent thickness of the central part is due to a downward projection of the lingual muscles to which the central part of the sublingua is closely applied (text-fig. 68 F).

The Lytta.—The tongue possesses a strong median ridge on the under surface of the sublingua, which Owen termed the "lytta." He did not describe sections of the tongue, for a well-developed lytta is present close to the sublingua. Gegenbaur made the same omission, but Nussbaum (**11**) recorded its presence. It is united to the upper surface of the sublingua in the median part of the latter. The condition resembles that of *Perodicticus*, in which there are lingual and sublingual lyttæ. In the latter species both lyttæ are internal. The position of the lytta in different parts of the tongue is seen in text-fig. 68 F.

Family TARSIIDÆ.

Genus TARSIUS.

THE TARSIER (*T. spectrum*).

The classical work of Burmeister (**2**) and the subsequent papers by Gegenbaur (**5**) and Pocock (**15**) have dealt with most points, so the work of any observer is now comparatively limited.

In the specimen in the Museum of the Royal College of Surgeons the shape of the tongue and the characters of the vallate, fungiform, and conical papillæ are similar to those described by Burmeister. That author does not mention that the lateral organs are absent. There is no great contrast between the conical papillæ on the oral part of the tongue and those on the base.

The sublingua is soft and defined from the under surface of the tongue by a groove only; it is the most adherent sublingua among the Prosimiæ. The median ventral rod does not terminate in a knob as in Pocock's specimen, but its free anterior extremity is rounded (text-fig. 69), and is slightly turned downwards as in *Chiromys*; as the specimen was preserved, I am unable to say whether this curving of the ridge was produced by the alcohol.

The frenal lamellæ are two conical tapering processes, and differ from the conditions recorded by Burmeister and Pocock.

Summary and Conclusions.

1. The tongues of the species of *Lemur* resemble those of the Chimpanzee and Gibbons in the **Y**-formation of their vallate papillæ, their convex lateral organs, and the contrast between the large conical papillæ on the pharyngeal part of the tongue and small ones on the oral part. They differ from the tongues of Man and the Orang-Outan in that the latter have no large conical papillæ on the base of the tongue, and their vallate papillæ form a **V**. They differ from the tongues of the Gorilla and Orang-Outan, whose lateral organs form ladder-like patterns on the dorsum of the tongue.
2. The tongue of *Microcebus* differs in the essential features from those of the species of *Lemur*, and resembles those of the Lorises, Galagos, and Pottos.
3. The tongues of the Lorisidæ and Galagidæ differ from those of *Lemur* in so many features that they are important for purposes of classification. Adding them to other characters

described by Pocock, Forsyth Major, and others, we obtain the following comparison:—

Lemur.	*Lorisidæ and Galagidæ.*
1. Vallate papillæ form a **Y**.	1. Vallate papillæ form a triangle.
2. Lateral organs convex.	2. Lateral organs absent.
3. Conical papillæ small on the oral part of the tongue and large on the base.	3. Conical papillæ increase gradually from the apex of the tongue to the epiglottis.
4. Sublingua triangular or lyrate, with apical denticles.	4. Sublingua tongue-shaped, with denticles along its anterior border.
5. Urethra opens above tip of clitoris.	5. Clitoris traversed by urethra.
6. Ectotympanic annular or horseshoe-shaped and inside bulla.	6. Ectotympanic external to bulla, of which it forms the outer wall.

I have not had the opportunity of examining the tongues of the Indrisidæ, but published accounts and illustrations ally them to those of *Lemur*.

4. The tongue of *Chiromys* has its own characteristic sublingua, which has a larger area free from the tongue than existing accounts lead one to expect. It has no lateral organs, but its basal conical papillæ are large. It has two or three vallate papillæ. Its characters resemble those of *Lemur* on the one hand and those of the Lorisidæ and Galagidæ on the other.

5. The tongue of *Tarsius spectrum* has the most adherent sublingua. It stands by itself in the consistence and size of the sublingua and the characters of its vallate papillæ.

6. The frenal lamellæ are frequently very complex, and supplementary lamellæ are present in *Nycticebus tardigradus*.

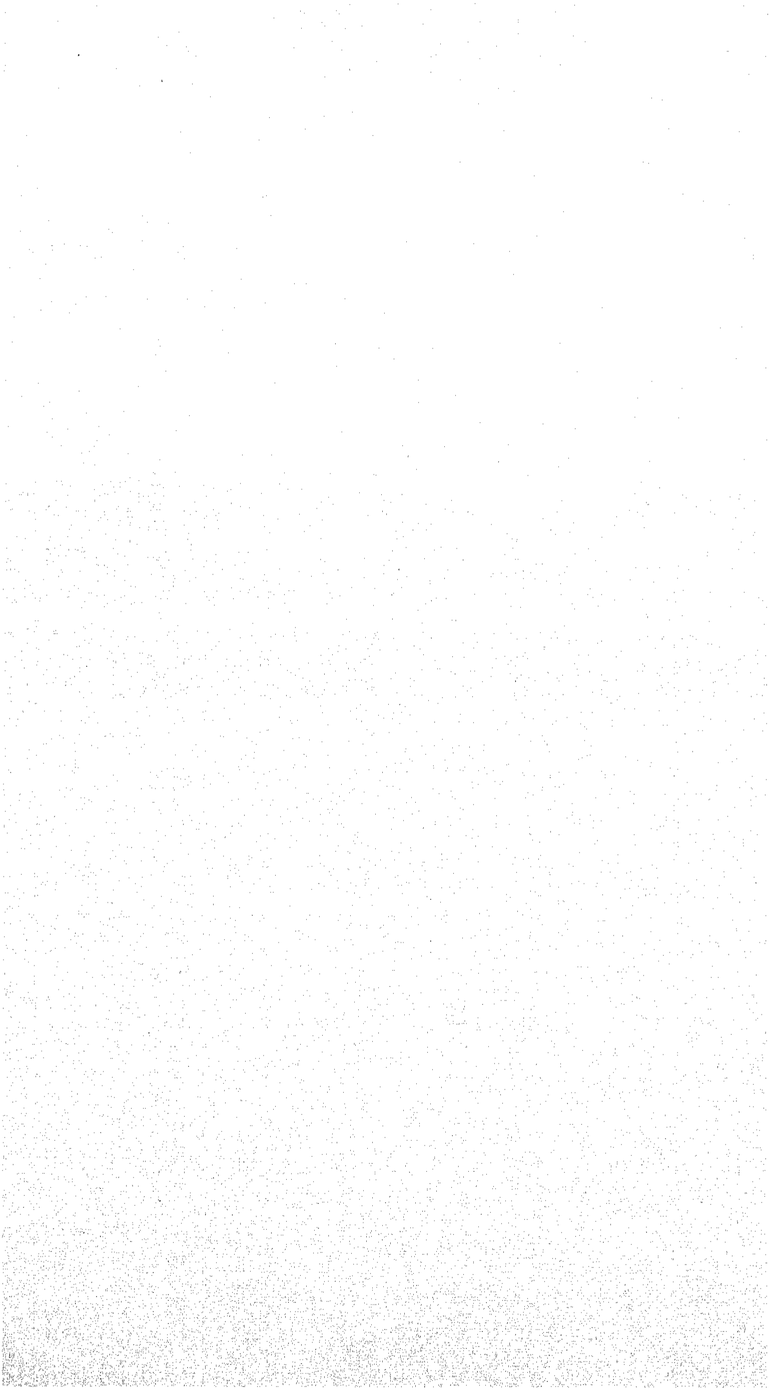
7. The foramen cæcum and Apical Gland of Nuhn are absent.

8. The lytta is present in several forms, and is frequently accompanied by a central axis, or lytta, of the sublingua. In the other Primates this is absent.

Bibliography.

1. Beddard, F. E.—"On some Points in the Structure of *Hapalemur griseus*." P. Z. S. 1884, p. 391.
2. Burmeister, H.—"Beiträge zur näheren Kenntnis der Gattung *Tarsius*." Berlin, 1846.
3. Campen, F. A. W. van.—Verhand. der König. Akad. van Wetenschappen, Amsterdam, 1859.
4. Flower, W. H.—"Lectures on the Anatomy of the Organs of Digestion of the Mammalia." Med. Times and Gazette, 1872.

5. Gegenbaur, C.—"Über die Unterzunge des Menschen und der Säugethiere." Morph. Jahrb. 1884, p. 428.
6. Hoeven, J. van der.—"Bijdrage tot de Kenntnis van den Potto van Bosman." Amsterdam, 1851.
7. Huxley, T. H.—"On the Angwántibo (*Arctocebus calabarensis*)." Proc. Zool. Soc. 1864, p. 314.
8. Kingma, P. H.—"Eenige Vergelijkend-Ontleedkundige Aanteekeningen over den *Otolicnus Peli*." Leyden, 1855.
9. Meckel, J. F.—System der vergleichenden Anatomie. Teil 4. Halle, 1829.
10. Münch, F.—"Die Topographie der Papillen der Zunge des Menschen und der Säugethiere." Morphol. Arb. 1896.
11. Nussbaum, J.—Anat. Anz. pp. 551–561, 1896; and pp. 345–358, 1897.
12. Oppel, A.—Lehrb. der vergl. mikr. Anat. vol. iii. pp. 251–270 and 391–393.
13. Owen, R.—"Monograph on the Aye-Aye." Trans. Zool. Soc. London, vol. v. p. 33, 1863.
14. Peters, W.—"Über die Säugethiergattung *Chiromys*." Abh. der Königl. Akad. der Wiss. zu Berlin, 1865.
15. Pocock, R. I.—"On the External Characters of the Lemurs and of *Tarsius*." P. Z. S. 1918, pp. 19–53.
16. Schrœder, J. L. C., van der Kolk, and W. Vrolik.—Bijdragen tot de Dierkunde, uitgegeven door het Koninklijk Zoologisch Genootschap "Natura Artis Magistra." Eerste Deel. Amsterdam, 1848–54.
17. Sonntag, C. F.—Papers on the Tongues of the Primates. P. Z. S. 1921, pp. 1–29, 277–322, 497–524.
18. Tiedemann, F.—Arch. f. Anat. u. Physiol. vol. v. pp. 348–356, 1819.
19. Tuckerman, F.—Journal of Morphology, vol. vii. pp. 69–94, 1891.
20. Sonntag, C. F.—P. Z. S. 1921, pp. 547–577.



39. The Comparative Anatomy of the Tongues of the Mammalia.—VI. Summary and Classification of the Tongues of the Primates. By Charles F. Sonntag, M.D., F.Z.S., Anatomist to the Society.

[Received August 8, 1921: Read November 8, 1921.]

Introduction.

In the five preceding papers of this series I described the structure of the tongues of the Primates and gave a short account of the physiology of the lingual glands. I also drew attention to a number of points bearing on the phylogeny of the tongue. In the present paper I have summarised these observations and pointed out how the lingual characters support systems of classification which have been based on external and skeletal characters.

Summary.

Pigmentation.—Most of the pigmented forms are included in the Cebidæ. The colour, which is yellow, green, brown or bluish-black, especially the latter, is uniformly distributed all over the dorsum, or the pigmented and colourless parts may form definite patterns; in *Ateles grisescens*, for example, there is a white cross on a brown background. The vallate and fungiform papillæ may be pigmented (e. g. in *Hylobates lar*) or colourless, but the lateral organs and central parts of the inferior surface of the tongue are always white. If several examples of each pigmented species are examined it will be seen that the colour varies considerably, so is of no value for purposes of classification. Most specimens of *Cercopithecus patas*, for example, have reddish-yellow tongues, but some tongues are colourless, and the fungiform papillæ of *Cercopithecus tantalus* are yellow or colourless. The bluish-black colour persists longest in preserving fluids.

Form and Proportions.—Most tongues are conical, but a few are oval, spatulate or rectangular; and shape is of no value for comparative purposes.

In most of the Primates the tongue is long and comparatively narrow, but in *Anthropopithecus troglodytes* and *Gorilla gorilla* the tongue of the young animal is relatively wider than that of the adult. I did not, however, see such variations in *Cercopithecus patas* or *Macacus sinicus*, of which I examined very young and adult examples.

Cunningham showed that the tongue of *Simia satyrus* resembles that of *Homo* most closely in the relative proportions of length and width.

The Apex is round, truncated or pointed, and may or may not have a notch, but the latter is usually absent from the fresh tongue. It is comparatively smooth, or roughened and tuberculated by small conical and fungiform papillæ. The relative quantities of fungiform papillæ on and immediately behind the apex vary; in the Simiidæ and Cercopithecidæ they are numerous and thickly clustered, but in the other families they are few and discrete.

In some species of *Lemur* the apex exhibits a number of sharp-pointed processes prolonged forwards from ridges on the inferior surface of the tongue, but these vary even in different examples of each species.

Sulci and Ridges.—Few fresh tongues have median dorsal sulci on the oral part of the dorsum, but many preserved specimens do; and I observed a well-marked median sulcus on the pharyngeal part in *Anthropopithecus troglodytes* alone. The most pronounced mesial dorsal sulcus which I observed occurred in *Mystax ursulus*. Median dorsal ridges are present in some Lemuroidea and Hapalidæ.

Wide, shallow transverse sulci separating low wide transverse ridges are present on the fresh tongues of *Lemur catta* and *Hapale jacchus*; and fine narrow sulci are seen in *Gorilla gorilla* and *Perodicticus potto*. Some of the fine sulci and ridges remind one of the patterns of fissures and ridges on the finger-tips.

The median ventral sulcus is present in most tongues, and is never an artefact induced by preserving fluids as is the dorsal one in bottled specimens. It is narrow and deep, or wide and shallow, and it frequently opens posteriorly into a triangular fossa which recieves the upper end of the frenum. In some of the Lemuroidea it receives the median dorsal crest of the sublingua, and it recesses the crest on the dorsal surface of the frenal lamella of *Cebus fatuellus*.

In *Gorilla gorilla*, some species of *Hylobates* and some of the Lemuroidea it contains a fixed crest; and it has been stated that the crest is a remnant of the sublingua, but the presence of both these structures in some Lemurs would seem to disprove that theory.

Lateral Borders.—The edges of the tongue are sharp, or full and rounded, and increase in thickness from before backwards in most species. Those of *Chiromys madagascariensis* are more massive in proportion to the size of the tongue than those of any other species of the Primates. Of the Pithecoids *Simia satyrus* and *Anthropopithecus* have the most massive lateral borders.

In *Tarsius spectrum*, *Microcebus*, *Chiromys*, and all Lorisidæ and Galagidæ the lateral borders are devoid of lateral organs and, as I hope to show in a future paper, this has an important bearing on phylogeny. In *Gorilla gorilla* and *Simia satyrus* only small parts of the lateral organs are found on the lateral borders, but in all other Primates the greater part is found there.

The conical and fungiform papillæ on the lateral borders are arranged in vertical rows and the points of the former are directed backwards.

Distribution of the Papillæ.—In all Primates except some specimens of *Simia satyrus* and *Symphatangus syndactylus*, some Lemuroidea and *Homo*, papillæ cover the entire dorsum, apex, lateral borders, and a bounding zone of the inferior surface. In all these species there are smooth non-papillary areas on the base of the tongue, and in the Lemurs the area is bisected by the median glosso-epiglottic fold.

The *ventral papillary zone* varies greatly in width, and its characters are of limited value for purposes of classification. It is wide in the Simiidæ, Cercopithecidæ, and in *Cebus*, *Ateles*, and *Lagothrix*, but is narrow or absent in all other Primates. In species with a wide zone the conical and fungiform papillæ are numerous, but in those with a narrow zone there are few or no fungiforms. In *Gorilla gorilla* many of the fine transverse sulci on the dorsum cut the lateral borders and run inwards on the ventral papillary zone.

The *Circumvallate Papillæ.*—In my paper on the tongues of the Cercopithecidæ I showed that all the papillary patterns present in the family will be seen in most species if sufficient examples of each are examined. The whole series may quickly appear or it may be necessary to examine many. I am not prepared, however, to apply this rule to any other family except the Hapalidæ, as insufficient specimens have come to hand.

In the following list of papillary patterns, P means two papillæ forming a pair, and D.P. indicates four papillæ arranged in a double pair. The Y type means that there are several papillæ present and does not include forms in which the four papillæ of a double pair are arranged in a Y.

Family.	*Patterns of vallate papillæ.*					
Simiidæ	Y.	T.	V.	Δ.		
Cercopithecidæ		T.	V.	Δ.		D.P.
Cebidæ			V.	Δ.	P.	D.P.
Hapalidæ				Δ.		
Lemuridæ	Y.			Δ.		D.P.
Lorisidæ				Δ.		
Galagidæ				Δ.	P.	
Chiromyidæ				Δ.	P.	
Tarsiidæ	Three papillæ arranged in a line.					

One can see, therefore, that the Simiidæ and Lemuridæ are the only families whose tongues possess more than four papillæ arranged in a Y, and it will be shown later that they differ from all other Primates in other respects.

The papillæ are round or oval on plan and conical on elevation, with the bases of the cones projecting beyond the vallums.

The *Fungiform Papillæ* stretch right across the dorsum, or are absent from the centre thereby forming a dorsal bounding zone. They form a cluster behind the apex, but are arranged in rows of varying degrees of obliquity behind that. The apical cluster is large in the Simiidæ and Cercopithecidæ, but in all other families the transverse rows extend far forwards at its expense. In the majority of tongues with large apical clusters there are many fungiform papillæ on the ventral papillary zone.

It has been shown by Tuckerman that the fungiform papillæ of the apical cluster have many taste-buds.

In some specimens of *Anthropopithecus troglodytes* there is a row of prominent fungiform papillæ occupying the mid-dorsal line of the tongue and replacing the median dorsal sulcus.

It is sometimes impossible to tell whether a papilla at the posterior part of the oral division of the dorsum is a large fungiform or small vallate form, for fossa and vallum may be indistinguishable even through a strong lens. Histological examination is the only proof. The fungiform papillæ may have no taste-buds or these, if present, lie on the free upper surface of the papilla; in the vallate papillæ, on the other hand, the taste-buds never lie on the free upper surface of the papilla, but are deep down on one or both sides of the fossa.

In some tongues there are more fungiform papillæ than are visible to the naked eye, for some are entirely concealed by overhanging conical papillæ (e. g. *Anthropopithecus troglodytes*).

The fungiform papillæ on the ventral zone may be thickly clustered at the apex of the tongue and scanty further back, or *vice versa*, and the examples, and the rows in which they are arranged are close together or discrete.

From the point of view of classification the most important features are the size of the apical dorsal cluster and the presence or absence of the fungiform papillæ on the ventral papillary zone. Although their presence or absence in the centre of the oral part of the dorsum varies greatly, it is not a character of sufficient distinctness to be of value for purposes of classification.

The *Conical Papillæ* vary in size and arrangement in the different families, and there are three types of the former:—

1. The papillæ on the pharyngeal part of the tongue are small:—*Homo*, *Simia satyrus*.

2. The papillæ on the oral part of the tongue are comparatively small, but those on the pharyngeal part are large and prominent:—*Gorilla gorilla*, *Anthropopithecus troglodytes*, all species of *Hylobates*, all species of *Lemur*, *Chiromys madagascariensis*, and *Tarsius spectrum*. This type also occurs in some lower Mammalia.

3. The papillæ gradually increase in size from the apex of the tongue back to the epiglottis:—Cercopithecidæ, Cebidæ, Hapalidæ, Lorisidæ, and Galagidæ. This arrangement is also present in *Microcebus* in which the vallate papillæ form a triangle, so the papillæ are of value for distinguishing it from *Lemur*.

The arrangement of the papillæ distinguishes most of the Cebidæ from all other families. In the latter they form a cluster behind the apex and rows of varying degrees of obliquity behind that, but in the Cebidæ they are dotted irregularly all over the dorsum.

The tongues with smooth non-papillary areas on the pharyngeal part of the dorsum have been enumerated above.

In most Primates the points on the oral part of the dorsum look backwards or backwards and inwards, but in some specimens of *Simia satyrus* and *Cercopithecus æthiops* those on the centre of the oral part run in all directions.

In the Cebidæ, Hapalidæ, Lemuroidea, and Tarsioidea the conical papillæ are mostly pointed, and cylindrical and globular forms are uncommon. In the other families there is a good admixture of all types.

The *Lateral Organs* present numerous forms and are of value for purposes of classification:—

1. Organs absent:—*Microcebus*, *Chiromys*, *Tarsius*, the Lorisidæ and Galagidæ.

2. The laminæ and sulci form ladder-like patterns on the dorsum of the tongue, and only their outer ends cut the lateral borders of the tongue:—*Gorilla gorilla* and *Simia satyrus*.

3. The organs are convex towards the lateral vallate papillæ:—*Anthropopithecus troglodytes*, *Hylobates* (all species), *Lemur* (all species).

4. There are rows of short laminæ and sulci on the lateral borders of the tongue:—Cercopithecidæ.

5. The inner borders of the organs are concave towards the lateral vallate papillæ:—Cebidæ.

6. A few faint irregular laminæ and sulci are present on the lateral borders of the tongue:—Hapalidæ.

In very few specimens did I find an equal number of laminæ and sulci in the two organs of the same tongue. But one must be careful not to mistake simple folds of the mucosa at either end of the organs for laminæ. Histological examination is the only true test in doubtful cases, for it reveals the presence of taste-buds in the true laminæ.

In a few species of *Cercopithecus* one may find fungiform papillæ situated on the laminæ of the lateral organs.

The degree of protrusion of the laminæ and depth of the sulci vary not only in different animals but in several examples of each.

The *Lingual Glands* are divided into apical and basal parts, but the former is most variable.

The *Apical Gland of Nuhn* is present only in *Homo* and *Simia satyrus*. Oppel believes that it is a piece which has become cut off from a forward prolongation of the basal glandular mass. The basal mass in the Marsupialia sends forwards two prolongations of variable stoutness, and it is possible that the Apical Gland of Nuhn has been cut off from one of these. If that were so it would support Gegenbaur's view that the tongues of the Primates have evolved from those of the Marsupialia.

The serous and mucous glands on the pharyngeal part of the tongue are developed to an equal degree in the Primates, but the degree of development of the entire basal mass varies.

The pharyngeal part of the tongue possesses a variable degree of development of lymphoid nodules, and a variable number of orifices of pits and the ducts of glands; and the latter are of value for distinguishing the tongues of the various genera of the Cercopithecidæ from one another. Orifices are visible in all Cercopithecidæ, but are absent from most Cebidæ, so are of classificatory importance when taken in conjunction with the characters of the lateral organs and mode of arrangement of the conical papillæ. The following are the characters of the orifices in the Cercopithecidæ:—

Genus *Presbytes*:—Orifices larger and more patulous than in any other genus, and lie in the centres of large round glandular areas. The salivary glands are enormous.

Genus *Cercopithecus*:—Orifices well-marked, discrete and not patulous, and no white areas present around them.

Genus *Macacus*:—Orifices like pin points.

Genus *Cercocebus*:—Small duct orifices present at the sides of the base of the tongue.

Genus *Papio*:—Large duct orifices present at the sides of the base of the tongue.

In many of the Cebidæ the nodules on the base form zones, with concave anterior borders, in front of the epiglottis, but I did not observe a similar condition in any other family.

The *Frenal Lamella* varies greatly in the Primates, and appears to belong to the floor of the mouth rather than to the tongue. It varies even in several examples of the same species, so is of limited value for purposes of classification.

In *Homo*, *Simia satyrus*, and some specimens of *Symphalangus syndactylus* it appears as two simple folds over Wharton's Ducts; but Mr. Pocock informs me that he observed two well-marked processes in a young *Simia satyrus*. I cannot believe, however, in conformity with my observations on the tongues of other animals, that reduction in the lamella is a change due to advancing years. In other species the lamella appears as a triangular or tongue-shaped process with an entire or divided apex and with both edges entire, serrated, or bearing small sharp points. The sharpest and most prominent points on the edges occur in *Cercopithecus preussi* and some specimens of *Cebus fatuellus*.

The *Orifices of Wharton's Ducts* vary in their position on the lamella as follows:—

1. On the upper surface—*Gorilla gorilla*.
2. On the apex—*Anthropopithecus troglodytes*.
3. On the under surface—*Pithecia satanas*.

The apical position is the commonest form, however.

Tuckerman described a rich nerve plexus with peripheral nerve endings in the lamella of *Ateles ater*, and Gegenbaur considered that the endings were tactile in function. As this condition has not been found in any other tongue there is insufficient material in which to work out its phylogenetic significance.

The *Sublingua.*—The various Lemuroidea are differentiated from one another by the shape, mobility, and characters of the crests and denticles as follows:—

1. Sublingua triangular or lyrate, has three ventral crests, and is very mobile. The apex is divided into a brushwork of denticles:—*Lemur*, *Hapalemur*, Indrisidæ.

2. Sublingua a large flat plate adherent to the under surface of the tongue by its central parts; no denticles present, but a strong keel-like ridge on its under surface projects forwards in the middle line:—*Chiromys.*

3. Sublingua large, tongue-shaped, but not quite so free as that of *Lemur*. There is only one median ventral crest, but the dorsal surface has a crest of variable prominence. This crest, the characters of the denticles, and the variations in the consistence of various parts of the sublingua are important:—

In *Microcebus* the sublingua is uniformly thick, the median dorsal crest is slight, and the denticles are moderately long.

In *Nycticebus* and *Loris* the central parts of the sublingua are thicker than the lateral parts, the median dorsal crest is small and the denticles are of moderate length; they are discrete in the former and close in the latter, but there is no essential difference between the sublinguæ of these genera.

In *Perodicticus* the median ventral crest is bifurcated posteriorly, the median dorsal crest is very prominent, and the denticles are long and slender.

In *Microcebus*, *Galago*, and *Hemigalago* the anterior border of the sublingua is broad, but in *Loris* and *Nycticebus* it is more or less pointed.

The *Plicæ Fimbriatæ* of the Simiidæ are derived from the sublingua by a process of phylogenetic reduction, and I showed that the plicæ of *Anthropopithecus troglodytes* with the intervening piece of mucosa form a soft triangular field resembling a sublingua; this is even more marked in the tongue of the new-born child, as described and figured by Gegenbaur. The plicæ of *Phascolarctos cinereus*, however, do not bound such an area.

The tongues of the Gibbons, Cercopithecidæ, Cebidæ, and Hapalidæ illustrate the ultimate stage of reduction, for no traces of the sublingua or plica are present as a rule in the extra-uterine stage. In the fœtal Gibbon, as shown by Deniker, there is a well-marked sublingua; and I observed two minute plicæ in a young *Cercopithecus patas*, so it is probable that the fœtuses of all Primates have sublinguæ.

If one examines a series of human tongues at different ages, one finds that the new-born child has well-developed plicæ or an actual sublingua provided with taste-buds. As age advances the buds disappear and the plicæ diminish in size. These taste-buds probably account for the more acute sense of taste in the child. Experimental methods also demonstrate that the sense of taste elicited by applications of solutions to the centre of the oral part of the dorsum diminishes as age advances.

This atrophy of structure following loss of function may have played an important part in the reduction in and ultimate loss of the primitive Mammalian tongue.

The Lytta.—Two forms are to be recognised:—The lytta of the tongue and the lytta of the sublingua. And Gegenbaur showed that the latter, when present, appears in one of two forms. In *Stenops* it forms a strong central supporting rod, but in *Tarsius* it is double. In *Lemur* it is absent altogether. Owen described the keel on the ventral surface of the sublingua as the lytta, but sections through the tongue show a well-marked lytta inside; it is connected in the middle to the sublingua.

CLASSIFICATION.

The structures which are of value for purposes of classification are:—

1. The number and arrangement of the vallate papillæ.
2. The arrangement of the conical papillæ on the oral part of the dorsum.
3. The mode in which the conical papillæ increase in size from before backwards.
4. The size of the cluster of fungiform papillæ on the dorsum behind the apex of the tongue.
5. The characters of the lateral organs.
6. The width of the ventral papillary zone, with the number, characters, and arrangement of its papillæ.
7. The presence or absence and characters of the lyttæ of tongue and sublingua.
8. The presence or absence of the apical gland of Nuhn, and the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum
9. The sublingua and plicæ fimbriatæ.

These features are of specific value in the case of all the Simiidæ, except *Hylobates*, and many of the Lemuroidea, but they are of generic value only in all other Primates. They lend additional weight to some schemes of classification based on external and skeletal characters; in some cases they help us to settle points which are not supported by a large body of very conclusive evidence.

The tongue of *Simia satyrus* resembles that of *Homo* most closely. Both have rounded apices, and their form and general proportions are similar. They have no large conical papillæ on the base of the tongue, and their vallate papillæ form a V. The frenal lamellæ are two small folds over Wharton's Ducts, and their plicæ fimbriatæ are equally developed, but smaller than those of other Primates; and they are the only Primates possessing an Apical Gland of Nuhn. In *Simia satyrus* the lateral organs are better developed, and the conical papillæ on the oral part of the dorsum include more pointed forms, but *Homo* alone of all the Primates possesses a foramen cæcum.

The ladder-like patterns formed by the lateral organs distinguish *Simia satyrus* and *Gorilla gorilla* from all other Simiidæ which have organs convex towards the lateral vallate papillæ, but the tongue of *Gorilla gorilla* has enormous conical papillæ on the pharyngeal part of the tongue, large plicæ fimbriatæ, a median ventral crest, and a large triangular frenal lamella; it has no Apical Gland of Nuhn, and its vallate papillæ form a V or Y.

The only character which really differentiates *Anthropopithecus troglodytes* on the one hand from *Hylobates* and *Symphatangus* on the other is the possession of plicæ fimbriatæ, for there is a similarity between them in all other features; and *Hylobates* has a well-marked, triangular, bifid lamella, whereas *Symphatangus syndactylus* has two small folds over Wharton's Ducts similar to those of *Homo* and *Simia satyrus*. Their vallate papillæ form a Y.

In the Cercopithecidæ, Cebidæ, and Hapalidæ the vallate papillæ never form a Y, the conical papillæ on the base of the tongue are never disproportionately large, and the lateral organs are neither ladder-like nor convex towards the lateral vallate papillæ. The chief differences between them lie in the characters of the lateral organs, the size of the apical cluster of fungiform papillæ, and the mode of arrangement of the conical papillæ on the oral part of the dorsum.

In the Cercopithecidæ the lateral organs form rows of laminæ and sulci on the lateral borders, the apical cluster of fungiform papillæ is large, and the conical papillæ on the oral part of the dorsum are regularly arranged. The genera are distinguished by the characters of the orifices of ducts and pits on the pharyngeal part of the dorsum (page 762).

In the Cebidæ the inner borders of the lateral organs are concave towards the lateral vallate papillæ, the conical papillæ on the oral part of the dorsum are crowded together without any definite arrangement, and the apical cluster of fungiform papillæ is small.

The vallate papillæ are two in number, and there is a well-marked median sulcus on the pharyngeal part of the dorsum in *Aotus*, but in all other genera there are more than two vallate papillæ, but no basal dorsal sulcus.

The ventral papillary zone is wide, and has few fungiform papillæ in *Lagothrix*, but it has many papillæ in *Ateles* and *Cebus*. In *Ateles* the ventral fungiform papillæ are most numerous round the apex, but in *Cebus* they are most numerous farther back.

The ventral papillary zone is narrow in *Pithecia*, *Alouatta*, *Callicebus*, and *Cacajao*. It has many fungiform papillæ in *Pithecia* but few or none in the others; and *Alouatta* is the only genus possessing large glandular orifices on the base of the tongue. *Callicebus* has many nodules and few orifices on the base, but *Cacajao* has neither.

The Hapalidæ always have a vallate triangle and a few irregular laminæ and sulci in their lateral organs. The pharyngeal part of the tongue occupies a relatively small part of the whole, and the ventral papillary zone is small or absent. The conical papillæ are regularly arranged and the apical cluster of fungiform papillæ is small. The lingual characters are not sufficiently distinctive to classify the genera.

The Lemuroidea and Tarsioidea differ from the Simiæ in the possession of a sublingua whose size, consistence, mobility, denticles, and minute structure vary in different families.

In the Tarsioidea the sublingua is soft, small, devoid of denticles, and only delimited at the sides from the under surface of the tongue by a narrow groove. There are no lateral organs, no large conical papillæ, and few apical fungiform papillæ.

In the Lemuroidea the sublingua is large, horny, denticulated, and is more or less movable.

In *Lemur* and *Hapalemur* the sublingua is triangular or lyrate, very free, and has three ventral crests. No lytta is present. The vallate papillæ form a Y, and the conical papillæ on the base are disproportionately large. The lateral organs are convex towards the lateral vallate papillæ.

In *Chiromys* the sublingua is tongue-shaped, adherent by its central parts, has one ventral crest which is keel-like and nodulated. It has a lytta inside the tongue. Vallate papillæ form a pair or triangle, but never a Y. Conical papillæ on base of tongue large. No lateral organs.

In *Microcebus*, the Lorisidæ and Galagidæ the sublingua is a flat plate with one median ventral crest and a variable dorsal crest. It varies in mobility, consistence, and denticles, and the value of these characters has already been described (page 763). The vallate papillæ form a triangle, but never a Y, the conical papillæ on the base of the tongue are not disproportionately large, and lateral organs are absent.

The special points arising from these notes on classification are :—

1. The tongue of *Simia satyrus* resembles that of *Homo*.
2. *Simia satyrus* and *Gorilla gorilla* differ from all other Simiidæ in the characters of the lateral organs, but there the resemblance between these two species stops.
3. The tongue of *Hylobates* differs from that of *Anthropopithecus troglodytes* in having no plicæ.
4. The separation of *Symphatangus* from *Hylobates*.
5. The great value of the lateral organs for purposes of classification.
6. The value of the lingual glands for distinguishing between the genera of the Cercopithecidæ.

7. The genera of the Hapalidæ cannot be distinguished from one another by the characters of the tongue.

8. The tongues of *Lemur* and *Hapalemur* resemble those of the Simiidæ most closely.

9. It is impossible to ally the tongue of *Microcebus* with those of *Lemur* and *Hapalemur*, but it resembles those of the Lorisidæ and Galagidæ.

10. The characters of the tongue at once distinguish the Lorises, Galagos, and Pottos from *Lemur*.

11. The tongue of *Tarsius* resembles neither those of the Simiidæ nor of *Lemur*, and is hard to distinguish from those of the Lorisidæ and Galagidæ. It has three vallate papillæ in a line, but these may be elements of a triangle which has been flattened out.

12. The keel on the under surface of the sublingua is not the true lytta as described by Owen.

40. On some new Parasitic Mites.

By Stanley Hirst, F.Z.S.

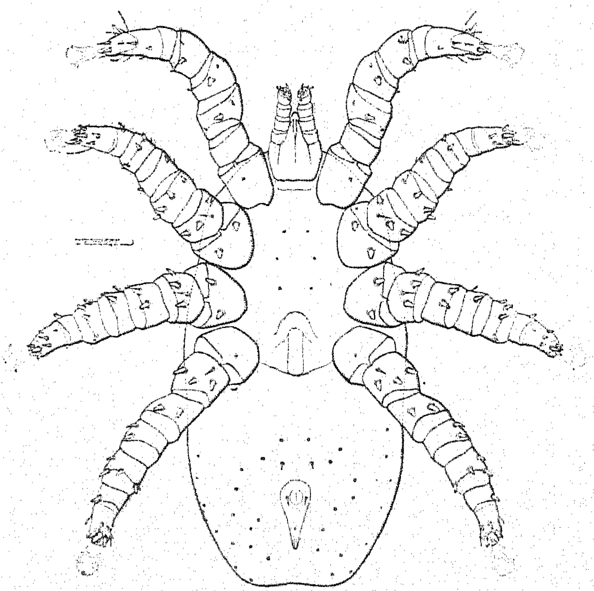
(Offered for publication by permission of the Trustees of the British Museum.)

[Received September 18, 1921; Read October 18, 1921.]

(Text-figures 16–43.)

The present paper deals with various parasitic Acari, mostly belonging to the family Gamasidæ, including eight new species of *Liponyssus* and a new species of *Rhinonyssus*, also two new genera closely allied to *Rhinonyssus*. A new Tarsonemid mite belonging to the genus *Podapolipus* is also described, and a new "Red Spider" (*Paratetranychus trinitatis*) found on grapes at Trinidad.

Text-figure 16.



Rhinonyssus novæ-guineæ, sp. n., ♀. Ventral view.

Genus Rhinonyssus Trouessart.

Rhinonyssus novæ-guineæ, sp. n. (Text-fig. 16.)

♀. Abdomen not elongated. The spinules or hairs usually present on the venter in this genus have practically disappeared, being mostly replaced by exceedingly minute and inconspicuous circular pores. *Anal plate* distinct, being elongate pyriform; it is furnished with a pair of hairs. Second and third coxæ each with a pair of very stout cones or tubercles; the other segments of the legs are provided ventrally with similar stout cones and also a few spinules.

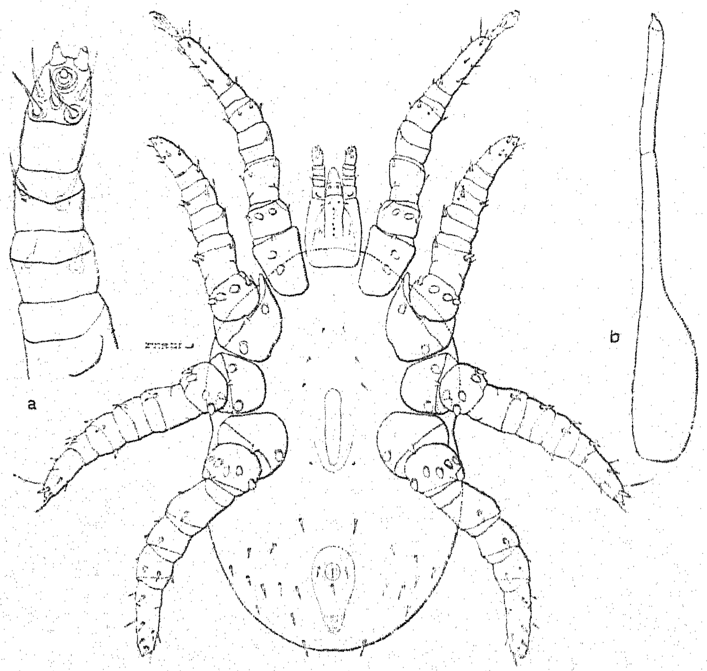
Length (including capitulum) ·93 mm.

Host: A bird (*Craspedophora magnifica*), New Guinea. Professor Trouessart's collection.

RHINONYSSOIDES, gen. nov.

Closely allied to *Rhinonyssus* Trouessart, but the chelicera is very differently shaped, consisting of a short stout basal portion and a long thin distal style, the latter has a very minute lobe near the distal end, which is very slightly curved, being in the form of a minute claw-like denticle (text-fig. 17 *b*).

Text-figure 17.



Rhinonyssoides trouessarti, sp. n., ♀. Ventral view.
a. Palp from below. **b.** Chelicera.

RHINONYSSOIDES TROUESSARTI, sp. n. (Text-fig. 17.)

♀. *Body* shaped as in *Rhinonyssus*, the abdomen not elongated however. Anterior hairs on venter short but quite fine. A number of hairs are situated posteriorly on the venter; they are longer than the anterior pairs of hairs and are fairly slender, the basal half being only slightly thickened, whilst the apical half is fine. *Anal plate* present, being pyriform in shape and furnished with three hairs as in *Liponyssus* etc. First free segment of palp apparently with a process. There is a median row of minute denticles on the ventral surface of the base of the capitulum. Anteriorly the second coxa is produced to form a stout process or spur rather similar to that present in the same position in *Liponyssus* but thicker and blunter. The spinules or hairs present on the proximal segments of the legs in *Rhinonyssus* are replaced by curious globular structures in this species; a pair being situated on each of the first three coxæ and a single globule on the fourth coxa. Trochanter of first leg with two chitinous globules ventrally, second and third trochanters each with three globules and a short pointed spinule, fourth trochanter with four globules and a short pointed spinule. Distal segments of legs furnished with short pointed spinules. Claws of first legs only slightly curved (the claws of the other legs are missing in the unique specimen).

Length (with capitulum) ·92 mm.

Host: A bird (*Sphecotheres maxillaris*), Australia. Professor Trouessart's collection.

NEONYSSUS, gen. nov.

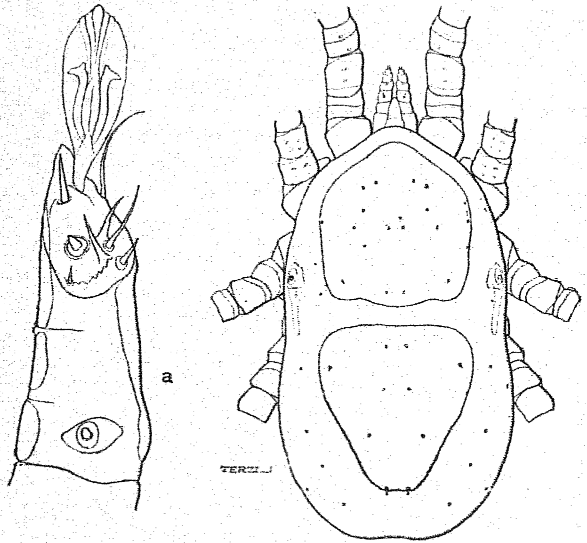
Allied to *Liponyssus* but with the palpi shorter, the sternal plate longer than wide, and the hairs on the body and legs very few in number. Differing from *Rhinonyssus* in the presence of two dorsal shields (an anterior and a posterior one), instead of only a single anterior shield.

NEONYSSUS INTERMEDIUS, sp. n. (Text-figs. 18, 19.)

♀. Two *dorsal shields* both fairly large, their surface reticulated and with numerous punctations, posterior shield with the hinder end rather bluntly rounded off. *Sternal shield* longer than wide, apparently there are no hairs on it, but there are three minute dots or circles on each side. *Genito-ventral plate* unusually short. *Anal plate* similar to that of *Liponyssus*, being pear-shaped. *Palpus* short, being very similar to that of *Rhinonyssus*. Apparently there is no median groove on the ventral surface of the capitulum. With the exception of the pair on the anal plate there seem to be no spines or hairs on the ventral surface. *Peritreme* opening dorsally as in *Rhinonyssus*. Legs rather short, apparently only the distal segments are furnished with hairs, a dorsal hair on the tarsus of the third leg being longer than the others, but still it is not very long; there is also a pair of distal spines on the ventral surface of this segment. Except for the dorsal spur on the anterior surface of the second coxa which is present but quite short (obsolete), the coxæ are without hairs or spines.

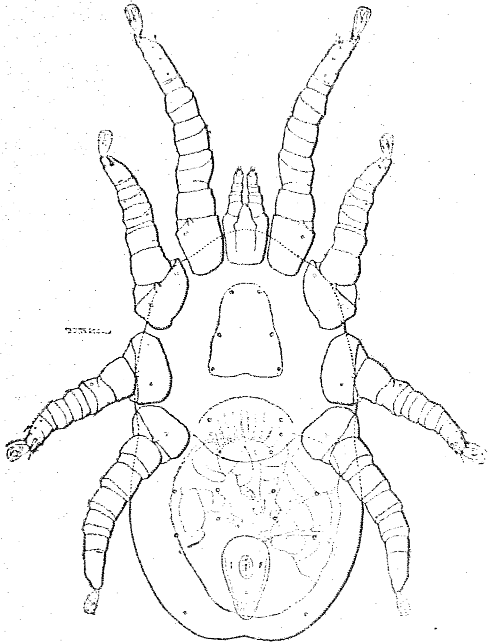
It is possible that some of the hairs on the body and limbs of

Text-figure 18.



Neonyssus intermedius, sp. n., ♀. Dorsal view.
a. Tarsus of first leg from above.

Text-figure 19.



Neonyssus intermedius, sp. n., ♀. Ventral view.

the single specimen have been destroyed by the caustic potash used in preparing it. It seems probable, however, that this absence is natural for in general appearance the mite is very like a *Rhinonyssus*, and the spines may be reduced or almost suppressed in the latter genus. There is a fully-developed larva inside the specimen and it resembles the parent in having only a few hairs on the legs. The claws of this larva are well developed and strongly curved.

Length (with capitulum) ·53 mm.

Host: The above description is based on a single specimen labelled "Sur un Oiseau de Madagascar." Professor E. L. Trouessart's collection.

Genus LIPONYSSUS Kolenati.

The species of this genus are found both on birds and mammals. Only the species that I have been able to examine personally are included in the key given below. A number of species are not in our collection, and these have been left out. Two dorsal shields are present in the nymphal stages of *Liponyssus*, whereas there is usually a single undivided dorsal shield in the adults. In the adult females of a few species, however, there are two dorsal shields as in the nymphs: for instance in *L. viator*, sp. n., where they are shaped exactly as in the nymphs of certain other species. The adult females can always be distinguished by the presence of separate sternal and genito-ventral plates on the venter, and by the delicate fan-shaped or semi-circular genital operculum situated at the front end of the latter plate.

Key to the females of the species of the genus *Liponyssus* present in the British Museum Collection:—

1.	Dorsum with two shields	2.
	Dorsum with a single shield	8.
2.	Posterior of the two dorsal shields very small	3.
	Posterior of the two dorsal shields fairly large	4.
3.	Anterior dorsal shield small and separated from the minute posterior shield by a considerable space	*L. serpentium* Hirst.
	Anterior dorsal shield rather long and only separated from the posterior one by a short space	*L. natricis* Gerv.
4.	Sternal plate quite short, the two posterior hairs on it long. Anterior spur on second coxa short	*L. viator*, sp. n.
	Sternal plate longer	5.
5.	Posterior margin of sternal plate strongly chitinised	6.
	Posterior margin of sternal plate weakly chitinised	7.
6.	Posterior dorsal shield with only three pairs of fairly long hairs	*L. chiropteralis*, nom. nov.
	Posterior dorsal shield with a number of fairly long hairs	*L. nyassæ*, sp. n.

7.	Sternal plate with strong reticulate markings. A few of the hairs at the posterior end of the body longer than the other hairs	*L. biscutatus*, sp. n.
	Sternal plate smooth. Hairs at posterior end of body not much longer than the others	*L. javensis* Oudms.
8.	Genito-ventral plate truncate posteriorly and furnished with three pairs of hairs	*L. madagascariensis*, sp. n.
	Genito-ventral plate rounded off or pointed posteriorly	9.
9.	Sternal plate with a pair of well-defined circular stigma-like markings. Genito-ventral plate with three pairs of hairs	*L. sternalis*, sp. n.
	Sternal plate without any circular markings. Genito-ventral plate with only a single pair of hairs........	10.
10.	Sternal plate with the posterior margin thickened......	*L. æthiopicus*, sp. n.
	Sternal plate not thickened posteriorly	11.
11.	Coxæ of legs furnished with distinct dentiform spurs.	12.
	Coxæ of legs without any spurs, except an anterior dorsal one on the second coxa	18.
12.	Coxa of second leg with a very large curved outer spur	*L. creightoni* Hirst.
	Coxa of second leg without any very large outer spur.	13.
13.	Coxa of second leg with two posterior spurs	*L. sciurinus*, sp. n.
	Coxa of second leg with only one posterior spur	14.
14.	Second coxa with a large curved inner (anterior) spur ventrally. Second tarsus usually ending in two spurs, one of which is very stout	*L. liberiensis* Hirst.
	Second coxa without any anterior inner spur ventrally.	15.
15.	Only the anterior dorsal spur of the second coxa and a little outer posterior spur on the third coxa present	*L. blanchardi* Trouessart.
	Several other spurs present on the coxæ as well	16.
16.	Posterior end of dorsal scutum rounded off or blunt...	*L. arcuatus* C. L. Koch and *L. carnifex* C. L. Koch.
	Posterior end of scutum pointed	17.
17.	Second coxa with only a very short rounded spur posteriorly	*L. confucianus* Hirst.
	Second coxa with a large pointed spur posteriorly ...	*L. macedonicus*, sp. n.
18.	Posterior end of genito-ventral plate rather wide and blunt or rounded off	19.
	Posterior end of genito-ventral plate narrower and usually pointed	21.
19.	Anal plate rather angular in shape	*L. flavus* Kolenati.
	Anal plate pear-shaped, the sides being curved.........	20.
20.	Size larger. Dorsal shield elongated and rather narrow. Sternal plate comparatively long and without any distinct markings. Peritreme rather short	*L. ellipticus* Kolenati.
	Size smaller. Dorsal shield wider. Sternal plate shorter and with a few deep curved little impressions on each side in the anterior angles. Peritreme long.	*L. granulosus* Kolenati.

21.	Sternal plate with three pairs of hairs	22.
	Sternal plate with two pairs of hairs	23.
22.	Dorsal shield narrow, especially posteriorly (parasitic on rats)	*L. bacoti* Hirst.
	Dorsal shield wider (parasitic on hen)	*L. bursa* Berlese.
23.	Hairs on dorsum only slightly curved	*L. silviarum* Can. & Fanz.
	Hairs on dorsum very distinctly curved	24.
24.	Dorsal shield rather short. Anal plate rather wide and short	*L. lacertinus* Berlese.
	Dorsal shield more elongated. Anal plate narrower and longer	*L. saurarum* Oudmns.

Liponyssus natricis Gerv.

Liponyssus arabicus mihi described from a female specimen found on a lizard (*Agama adramitana*) is apparently identical with *L. natricis* Gerv. I have examined examples of the latter found on a snake at Florence kindly sent me by Prof. Berlese. A very minute posterior shield is present on the dorsum in the adult female, and Berlese seems to have overlooked it. It is very similar in shape to that present in *L. serpentium* mihi, but is longer and only separated from the anterior dorsal shield by a short space, whereas in the *L. serpentium* the two dorsal shields are widely separated from one another.

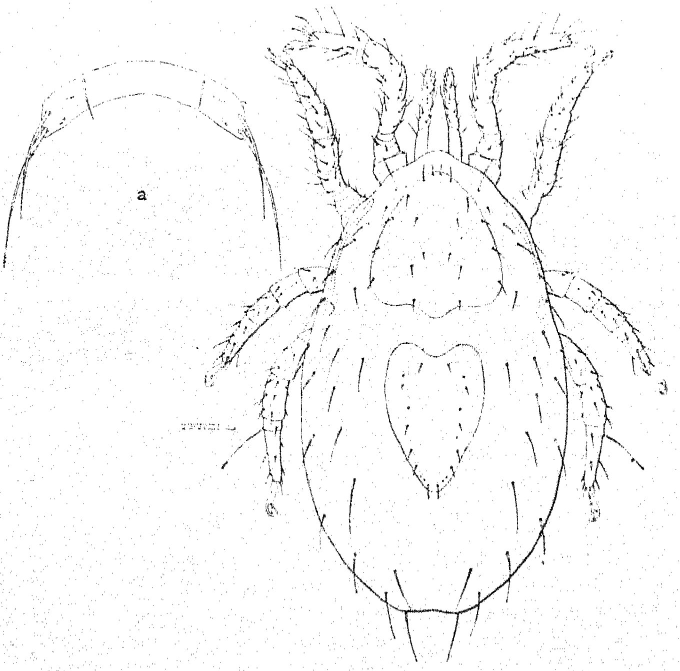
Liponyssus viator, sp. n. (Text-fig. 20.)

♀. There are two *dorsal shields*, shaped as shown in figure, the anterior one being slightly produced in the middle posteriorly, whilst the posterior one has the anterior margin rather strongly concave; posterior dorsal shield shaped rather like a tongue, the lateral margins being at first convex and then narrowing to form the bluntly pointed posterior end. Hairs on dorsal shields short, some of the hairs on the margins of the anterior dorsal shield are a little longer, and the hairs of the terminal pair on the posterior shield are longer than the others on its surface. Lateral hairs on body fairly long and the posterior hairs on uncovered part of dorsum very much longer than those on the shields. *Sternal plate* very short, being in the form of a narrow transverse strip; it bears three pairs of hairs, those of the anterior pair are much shorter than the posterior ones, the latter being much longer than usual. *Genito-ventral plate* narrow, the posterior end rather blunt. *Anal plate* pear-shaped. *Peritreme* reaching as far forwards as the middle of the second coxa or somewhat further forwards. A minute and inconspicuous spine or spur is present on the anterior surface of the second coxa, but it is much shorter than in most species of *Liponyssus*; the other coxæ apparently are without spurs. It is not easy to make out the denticle on the first free segment of the palp in the specimens from *Cypselus affinis*, but it is quite distinct in the example from *Gecinus vaillanti*, being sharply pointed.

Length of body (not including capitulum), ♀ ·65–·87 mm.

Host: Several specimens from nests of *Cypselus affinis*, Calcutta, collected by C. Paiva (28. vi. 1909) and forwarded to me by Dr. Nelson Annandale. Also an example from *Gecinus vaillanti*, Tangier (May 1892), presented to the Museum by Dr. James Waterston.

Text-figure 20.



. *Liponyssus viator*, sp. n., ♀. Dorsal view.
a. Sternal plate.

NOTE.—The specimen from *Gecinus vaillanti* agrees closely with those from *Cypselus affinis* in the structural details given above, but the posterior dorsal shield is rather more narrow, and the denticle on the first free segment of the palp distinct.

LIPONYSSUS CHIROPTERALIS, nom. nov.

♀. Two *dorsal shields* are present, their surface being finely reticulated. The shape of these shields varies somewhat in specimens from different localities; the posterior one is tongue-shaped, its hinder end being narrowed and blunt. Hairs on the shields of moderate length; there are three pairs of these fairly long hairs on the posterior shield and also three or four pairs of very minute and inconspicuous hairs at its posterior end. Hairs on softer parts of body very numerous, of moderate length and rather thick. *Sternal plate* trapezoidal, its posterior margin is very much thickened, being strongly chitinised as in *L. æthiopicus* and *L. nyassæ*; anterior pair of hairs on it quite short, the other two pairs usually longer. *Genito-ventral plate* with the posterior end sharply pointed. *Anal plate* pear-shaped. *Peritreme* only reaching as far forwards as the middle of the second coxa or even shorter. First free segment of *palp* with a well-developed process. Second *coxa* with the anterior spur well-developed; apparently there are no other spurs or spines on the coxæ. Bristles on dorsal surface of legs very numerous and rather stout.

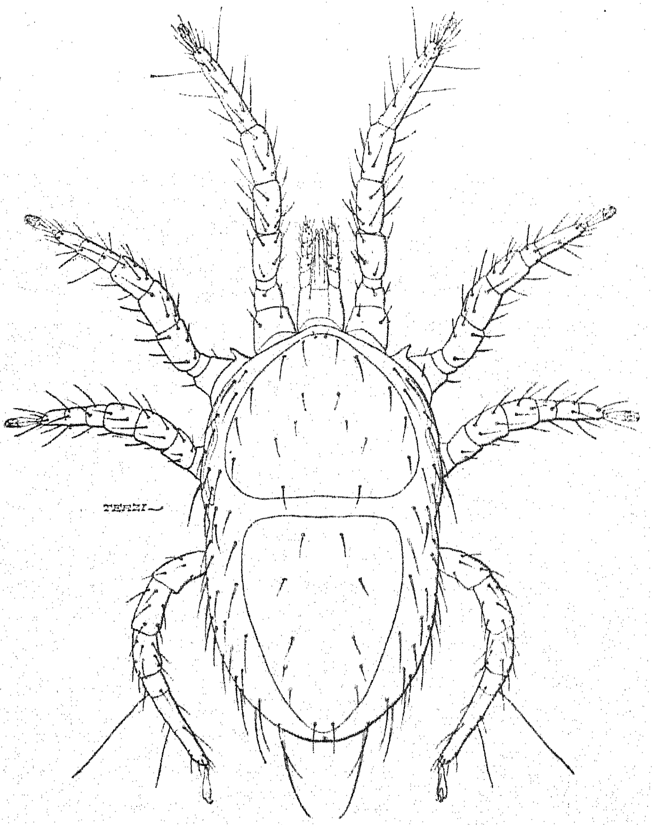
Hosts: Bats. On *Pipistrellus*, Ambleside, Windermere (11. iii. 1912) (*J. F. Cormack*); ex Dr. J. Waterston's coll. On *Myotis myotis*, Oristano, Sardinia (*Dr. A. H. Krausse*); ex Hon. N. C. Rothschild's coll. On bats, at Ain Sefra, S.W. Algeria (14. v. 1913); ex Hon. N. C. Rothschild's coll. Off *Ctenodactylus gundi*, Gorge of Tilaton, El Kantara; specimens collected by the Hon. L. W. Rothschild and Dr. E. Hartert. Also a specimen from a bat, Tabgka, Tiberias (*P. E. Schmitz*); ex the Hon. N. C. Rothschild's coll.

NOTE.—Canestrini, relying upon the colour of living specimens, considered this species of *Liponyssus* with two dorsal shields to be *L. arcuatus* C. L. Koch (see Prospett. Acar. Ital. i. pp. 120–121, 1885), and Berlese is also of this opinion in his Acari etc. Reprt. in Italia (Ordo Mesostigmata, p. 22, 1892). Oudemans gives the name *L. arcuatus* to quite a different species with an undivided scutum (see Arch. Naturg. Abt. A. Heft ix. pp. 68–75, 1913). According to this author the name of this species with two dorsal shields should be *L. musculinus* C. L. Koch—a mite found on the house-mouse (see Tijdschr. Ned. Dierk. Ver. (2) vii. p. 293, 1902). It is impossible to determine the two species said by Kolenati to have two dorsal shields, viz., *Steatonyssus periblepharus* and *S. brachypeltis* (see Sitzb. K. Akad. Wiss. Wien, xxxv. pp. 186 & 187, 1859). As it seems to be impossible to ascertain the real name of this mite, I propose the new name *L. chiropteralis* for it.

LIPONYSSUS NYASSÆ, sp. n.

♀. Two *dorsal shields* are present in this species, the anterior one being very wide; the posterior one is much narrower and shaped like that of *L. æthiopicus*, sp. n., and *L. chiropteralis*, being tongue-shaped and with the anterior margin distinctly concave. It differs from the posterior dorsal shield of *L. chiropteralis* in having a number of moderately long hairs on its surface instead of only three pairs as in that species. Hairs on uncovered (softer) part of dorsum numerous, stiff, of moderate length, and sharply pointed much as in *L. chiropteralis*. *Sternal plate* rather weakly chitinised except the posterior margin, which is very much thickened and slightly concave as in *L. chiropteralis* and *L. æthiopicus*; there are numerous fine transverse linear markings on its surface and the three pairs of hairs are long and fine. *Genito-ventral plate* with the posterior end rather bluntly

Text-figure 21.



Liponyssus biscutatus, sp. n., ♀. Dorsal view.

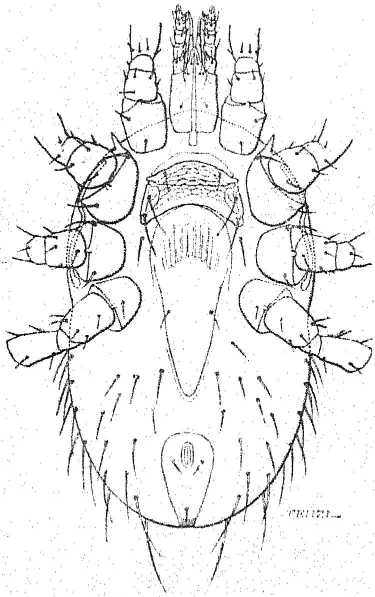
pointed, and it has only one pair of hairs on it. *Anal plate* pear-shaped. Hairs on *venter* numerous, fine and of moderate length. *Peritreme* extending a little further forwards than the middle of the second coxa. First free segment of *palp* with a ventral process. With the exception of the well-developed anterior spur on the second coxa, the coxæ are without spurs or spines. *Legs* furnished with numerous fine hairs or setæ.

Host: Elephant shrew, Chiromo, Nyasaland; ex Coll. of Imperial Bureau of Entomology.

LIPONYSSUS BISCUTATUS, sp. n. (Text-figs. 21, 22.)

♀. *Dorsal shields* two in number, both are fairly wide, the outline of the posterior one is shaped rather like a thimble or cone, the blunt apex of which is the posterior end. Hairs on scutum not numerous and arranged as shown in figure, those in the middle of its surface are short, but the ones on the margins of the anterior plate are longer. Hairs on softer part of dorsum much longer than those on the dorsal shields, a few at the posterior end of the body being considerably longer than the others. Hairs on venter fine and of moderate length. *Sternal plate* large and its surface is strongly reticulated; its posterior margin is concave; three pairs of hairs are present on it, the first pair being short and weak, the posterior pairs very long. *Genito-ventral plate* narrowed posteriorly to form a sharp point. *Anal plate* pyriform and rather longer than usual. *Peritreme* reaching as far forwards as the middle of the second coxa or slightly further. First free segment of the *palp* furnished with a strong pointed tooth-like process. Anteriorly the second coxa has the usual spur, otherwise the coxæ are devoid of spurs. Hairs on legs quite fine, none of them being spiniform.

Text-figure 22.



Liponyssus biscutatus, sp. n., ♀. Ventral view.

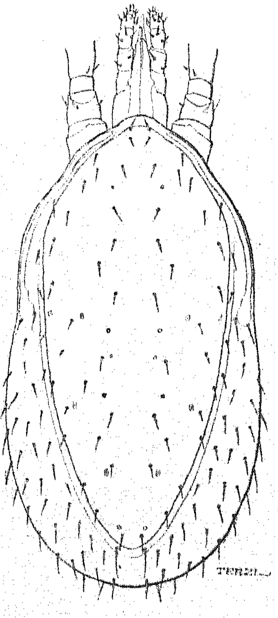
Length of body (not including capitulum) ·65 mm.

Host: *Dendropicus cardinalis*, South Africa.

LIPONYSSUS MADAGASCARIENSIS, sp. n. (Text-figs. 23, 24.)

♀. *Dorsal shield* shaped rather like that of *L. bursa* (see text-fig. 23), the hairs on its surface short, the terminal pair at the posterior end somewhat longer than the others. Hairs on the softer part of the *dorsum* numerous, they are short but mostly slightly longer than those on the shield. *Sternal plate* large, being longer than usual; it is trapezoidal in shape, the posterior margin being straight except in the middle where it is slightly concave; there are three pairs of hairs on it and they are rather short. *Genito-ventral plate* unusual in shape for a species of *Liponyssus*, for instead of being pointed or rounded off posteriorly it is truncated; also there are three pairs of hairs on it instead of only one pair, one pair being situated opposite the fourth coxæ, the two others at the posterior end of the plate, one of these pairs being placed on its posterior margin. *Anal plate* pear-shaped and more elongated than usual. *Peritreme* extending a little beyond the first coxa. Besides the usual dorsal spur, there is a ventral (inner) spine anteriorly on the second coxa, it is stout but curved. There is a similar anterior spine on the third coxa. Both the second and third coxæ are without any posterior spurs.

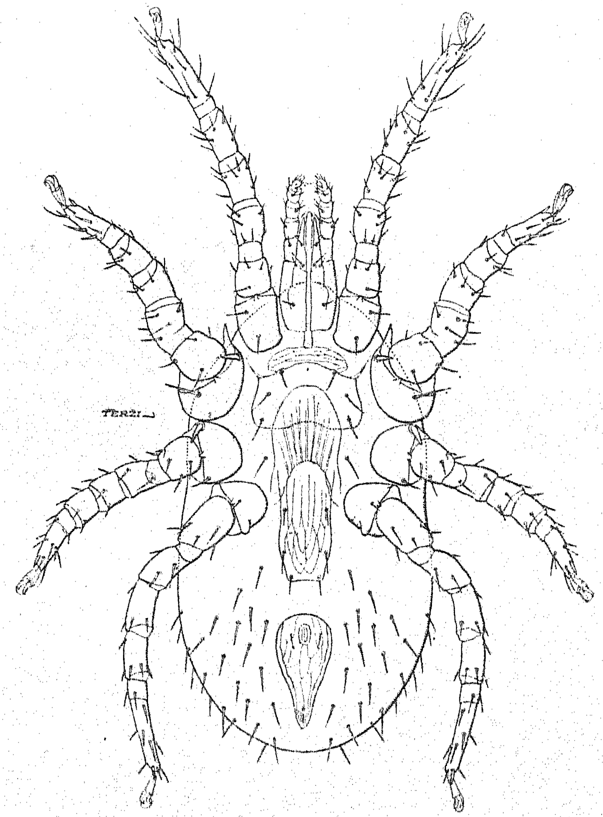
Text-figure 23.



Liponyssus madagascariensis, sp. n., ♀. Dorsal view.

There is, however, a short but blunt posterior spur on the fourth coxa. Legs furnished with hairs and bristles, there is a short spine ventrally at the distal end of the tarsi of the posterior legs.

Text-figure 24.



Liponyssus madagascariensis, sp. n., ♀. Ventral view.

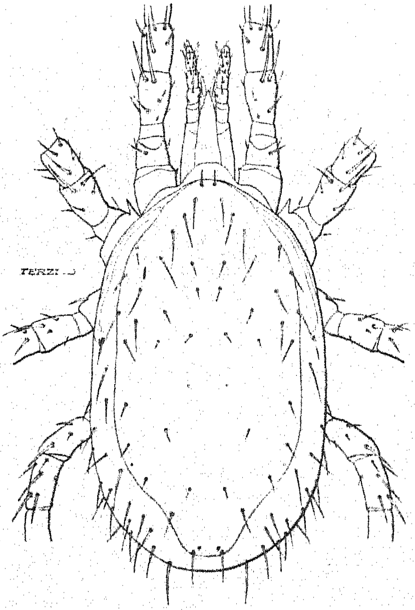
Length of body (not including capitulum), ♀ ·79–·96 mm.

Host: *Lemur mongoz* var. *albifrons*, Diego Suarez, Madagascar (*G. Melow*); ex the Hon. N. C. Rothschild's coll.

Liponyssus sternalis, sp. n. (Text-figs. 25, 26.)

♀. *Dorsal shield* large and undivided, it is much narrowed anteriorly, in the middle the sides are straight and parallel, posteriorly it is rather abruptly narrowed to form a short tail-like portion which is truncated posteriorly. Anterior hairs on scutum of moderate length and so are also two pairs at the posterior end, one pair being terminal, the rest of the hairs on its surface are very short. Hairs on soft uncovered part of dorsum of moderate length. *Sternal plate* trapezoidal in shape, its posterior margin slightly concave; on each side in the anterior angle there is a very well-defined circular mark consisting of an outer rim and a pitted interior; three pairs of hairs are present on the sternal plate and they are long and fine. *Genito-ventral plate* rounded off posteriorly and with three pairs of hairs on its surface, viz., the usual pair situated opposite the fourth coxæ and also two pairs at the posterior end of the plate, one of them being terminal. *Anal plate* large and pear-shaped. Hairs on venter very numerous and of moderate length. *Peritreme* extending forwards about as far as the middle of the first coxa. *Palp* ventrally with a lobe-like process on the first free segment as in *L. granulosus* etc. The usual anterior dorsal spur is present on the second coxa; there are also chitinous raised lines on the coxæ but no distinct spurs. There are numerous bristles on the legs, especially on the dorsal surface.

Text-figure 25.

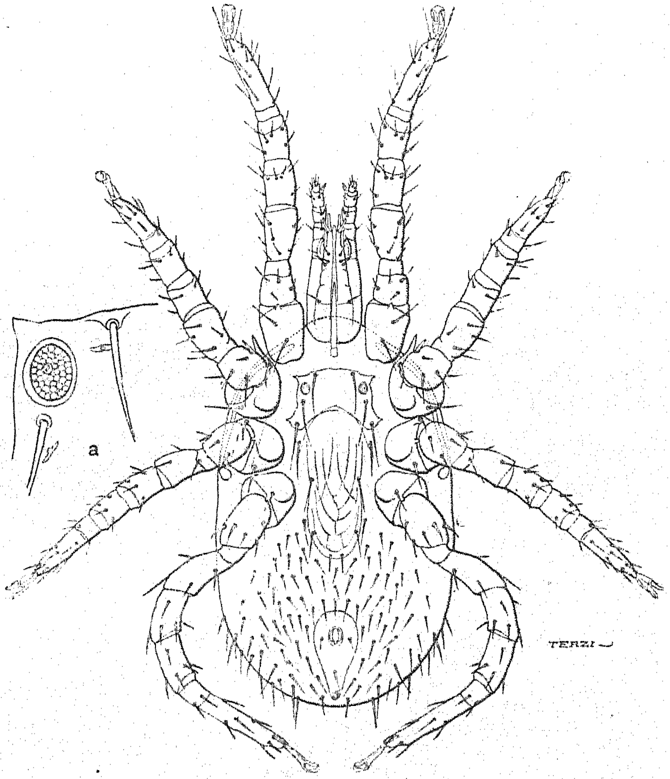


Liponyssus sternalis, sp. n., ♀. Dorsal view.

Length of body (not including capitulum) ·80 mm.

Host: A bat found in a cave near Lake Beshik, Salonika (27. v. 1918), Dr. James Waterston.

Text-figure 26.

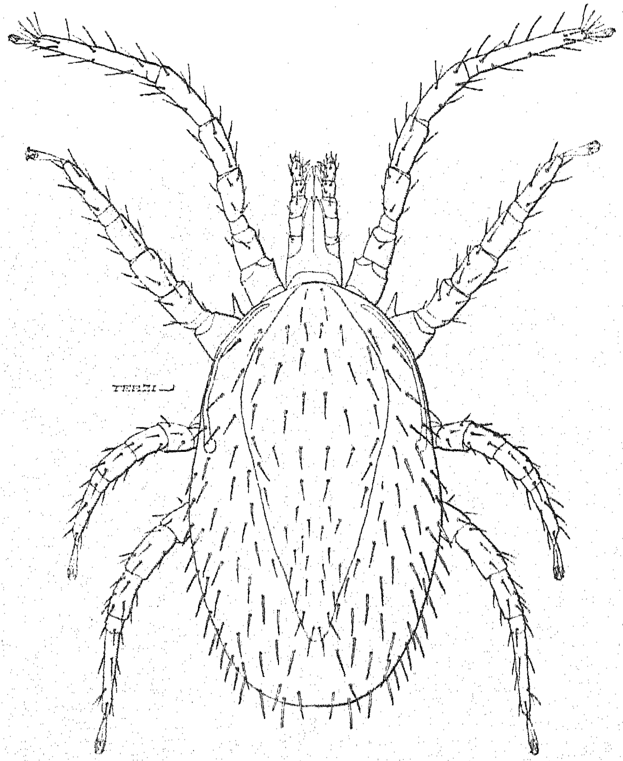


Liponyssus sternalis, sp. n., ♀. Ventral view.
a. Anterior angle of sternal plate greatly enlarged.

LIPONYSSUS ÆTHIOPICUS, sp. n. (Text-fig. 27.)

♀. *Dorsal shield* shaped as shown in text-fig. 27, being elongated and comparatively narrow; it is widest opposite the interval between the second and third legs, being narrowed anteriorly, whilst posteriorly it is still narrower gradually decreasing in width, and being rather drawn out and tapering, the end bluntly pointed. Hairs on its surface numerous; they are not very long and are usually plain, but some of them have a few inconspicuous hairlets. Hairs on uncovered part of dorsum also numerous; they are not much longer than those on the scutum, some of them are slightly bifid at the end and furnished with inconspicuous accessory hairlets, especially those at the hinder end of the body, which are also slightly stouter and blunter than the others. None of the posterior hairs are especially long. *Sternal plate* trapezoidal, not short, its surface finely reticulated; its posterior margin is much thickened and slightly concave. *Genito-ventral plate* narrowed and tapering to a point posteriorly. *Anal plate* pear-shaped. Hairs on venter rather numerous; they are finer and rather longer than those on the uncovered part of the dorsum. *Peritreme* reaching about as far forwards as the middle of the first coxa. Anteriorly the second coxa has a strong forwardly directed spine; otherwise the coxæ are devoid of spines or spurs. First leg long, especially the tarsus, the fourth legs also long; second and third legs much shorter, the former being rather stout. First free (proximal) segment of palp furnished with a process which seems rather flattened and not so spiniform as in some species.

Text-figure 27.



Liponyssus æthiopicus, sp. n., ♀. Dorsal view.

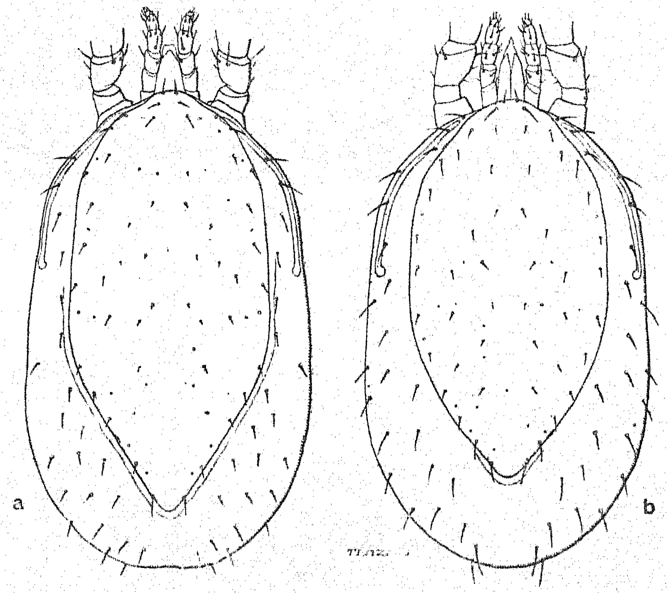
♂. *Ventral plate* with reticulate markings and rather narrow, being scarcely widened posteriorly; there are eighteen hairs on it arranged in nine pairs and also an unpaired posterior hair. The usual strong anterior spur is present on the second coxa. There is also a rather strong curved spine on the anterior margin of the third coxa. Bristles on legs mostly fine and none of them are very stout. *Peritreme* reaching the first coxa.

NOTE.—The male is described from specimens from the Sudan only.

Length of body (not including capitulum), ♀ ·61 mm. (distended female specimens up to ·98 mm.); ♂ ·43–·45 mm.

Hosts: Elephant shrew, Chiromo, Ruo River, Nyasaland, 1916 (*R. C. Wood*); ex Coll. of the Imperial Bureau of Entomology. Also off bats at Singa, Sennar Province, Sudan, 1913 (*Capt. W. E. Marshall*); ex the Hon. N. C. Rothschild's coll.

Text-figure 28.

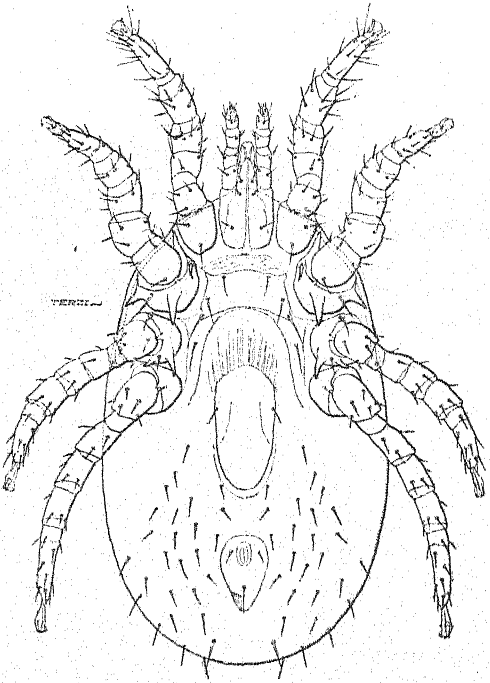


a. *Liponyssus sciurinus*, sp. n., ♀. Dorsal view.
b. *Liponyssus blanchardi* Trouessart, ♀. Dorsal view.

LIPONYSSUS SCIURINUS, sp. n. (Text-figs. 28 *a*, 29.)

♀. *Body* oval, being widest some distance before the posterior end, sometimes it is slightly bilobed posteriorly. *Dorsal shield* large and undivided, being shaped as shown in text-fig. 28 *a*, posteriorly it is evenly narrowed, the end being bluntly pointed. Hairs in middle of this shield exceedingly minute and fine, even the marginal hairs are quite short, the terminal posterior pair being, however, slightly longer than the others. Hairs on uncovered part of dorsum short and fine. *Sternal plate* longer than is the case in *L. carnifex* and *L. arcuatus*, the posterior margin being only slightly concave; the three pairs of hairs on its surface are fairly long. *Genito-ventral plate* of moderate width, its posterior end rounded off. *Anal plate* pear-shaped. Hairs on venter fairly numerous. Anterior (dorsal) spur of *second coxa* well-developed; there is also a little curved hook-like spur (or rather spine for it is articulated) on the inner surface of this coxa anteriorly, and *two large spurs or teeth on the posterior margin*, the outer one being almost as large as the inner. Third coxa also with two spurs on its posterior margin, but the outer one is much weaker than the inner. *Peritreme* extending forwards as far as the middle of the first coxa or a little further forwards. There are a number of subspiniform bristles on the distal segments of the legs; the paired stout little spurs or spinules present at the distal end of the second tarsus in

Text-figure 29.

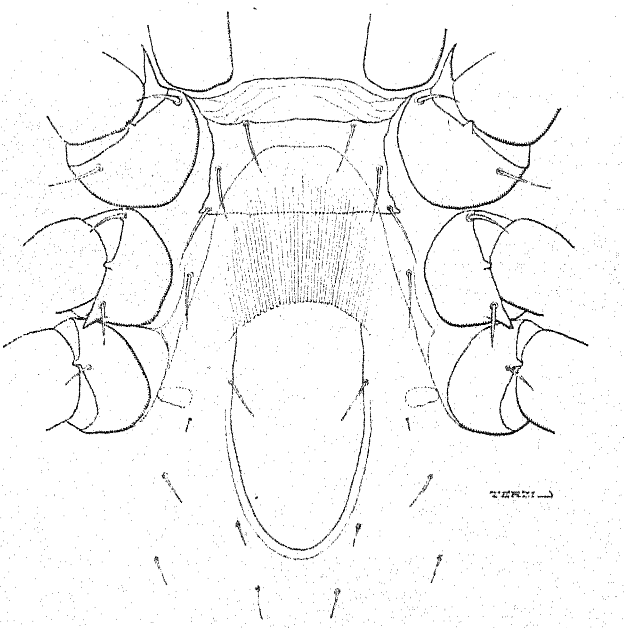


Liponyssus sciurinus, sp. n., ♀. Ventral view.

L. carnifex and *L. arcuatus* are absent in this species from squirrels.

♂. *Genito-ventral plate* rather slender and it has nine pairs of hairs on it, besides the unpaired posterior hair, it is not divided into two portions by a transverse line as is the case in *L. flavus* etc. *Peritreme* reaching as far forwards as the middle of the first coxa. Spurs and spines on the coxæ as in the female sex. At the distal end of the second tarsus there is a pair of very strong short spinules ventrally. Fourth leg not enlarged, the spiniform bristles on this limb are not very thick.

Text-figure 30.



Liponyssus blanchardi Trouessart, ♀. Ventral surface showing coxæ, sternal and genito-ventral plates.

Length, ♀ (including capitulum and palpi) ·83–·90 mm.; of body only ·73–·81 mm.; greatest width ·40–·42 mm.

♂. *Length* of body ·53 mm.; width ·31 mm.

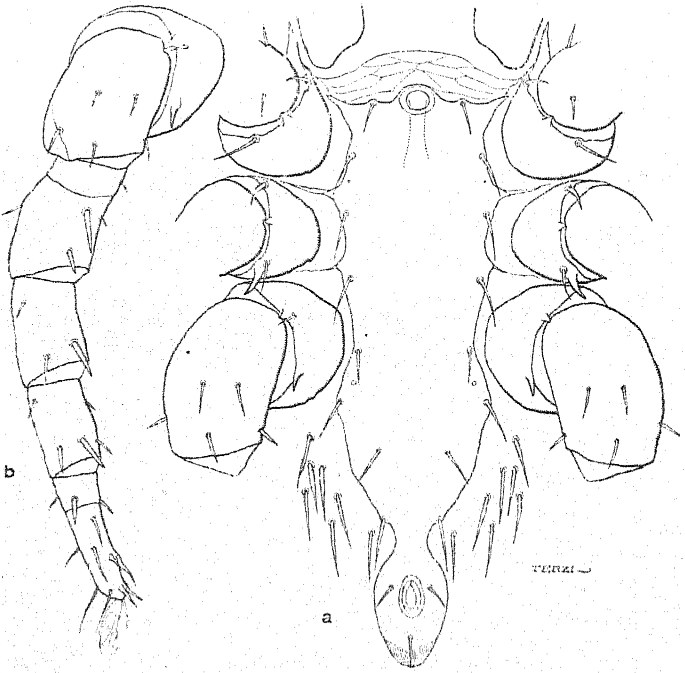
Host: Squirrels at Briançon, France (26. ix. 1887). Collection of the Paris Faculty of Medicine.

Liponyssus blanchardi Trouessart. (Text-figs. 28 *b*, 30, 31.)

Leiognathus blanchardi Trouessart, 1904, Arch. Parasit. viii. pp. 558–561, 2 text-figs.

♀. *Dorsal shield* large and undivided, narrowing posteriorly, the tip being blunt (almost pointed). Hairs on dorsal shield all short, but the marginal ones are longer than the others. Hairs on uncovered part of body about as long as the longest of the marginal hairs on the shield or somewhat longer, a few at the posterior end of the body are longer than the others, but still none of them are very long. *Sternal plate* trapezoidal, not very short, and furnished with the usual three hairs which are of moderate length; the posterior margin is straight. *Genito-ventral plate* of moderate width, the posterior end rounded off. *Anal plate* pear-shaped. Hairs on venter short and not very numerous. *Peritreme* reaching about as far forwards as the middle of the first coxa. With the exception of a distinct (outer) pointed tooth or spur on the posterior edge of the third coxa, and the usual anterior spur of the second coxa, the *coxæ* are devoid of spurs or teeth. None of the spines on the legs are very stout.

Text-figure 31.



Liponyssus blanchardi Trouessart, ♂.

a. Ventral surface showing coxæ and ventral plate.
b. Fourth leg greatly enlarged.

♂. *Ventral shield* becoming rather wide behind the last coxæ, its sides here being convex but afterwards narrowing to form the usual neck-like portion connecting with the anal part of the plate; the transverse line present on this plate in *L. flavus* and *L. granulosus* is absent in this species. There are nine pairs of hairs on the ventral plate and also the usual unpaired posterior hair. Besides these hairs on the plate itself there are a few lateral hairs posteriorly on the venter and they are fairly long. The curved anterior seta on the inner side of the third coxa is rather stout, being almost spiniform; this coxa has also a very slender outer posterior spur. Fourth coxa also usually with a very slender posterior spur. First leg more slender than the others, the second and third being short and stout; the fourth leg is enlarged as in *L. carnifex* C. L. Koch, some of the spines on this limb being rather stout, especially in the specimens from the Prairie Marmot. Second tarsus with a pair of distal spinules ventrally which are very stout and quite short.

Length. ♀ (without capitulum) ·73–·78 mm.; ♂ ·58–·63 mm.

Host: Alpine Marmot. The above description is based on a number of female specimens mounted on a slide (one of Professor Blanchard's preparations in the collection of the Paris Faculty of Medicine). Also examples of both sexes taken on marmots at Zermatt (*M. Biner*); ex N. C. Rothschild's coll. Also examples of both sexes from specimens of the Prairie Marmot (*Cynomys ludovicianus*) bred by Sir E. Loder at Leonardslee, Horsham, England.

LIPONYSSUS CONFUCIANUS, nom. nov.

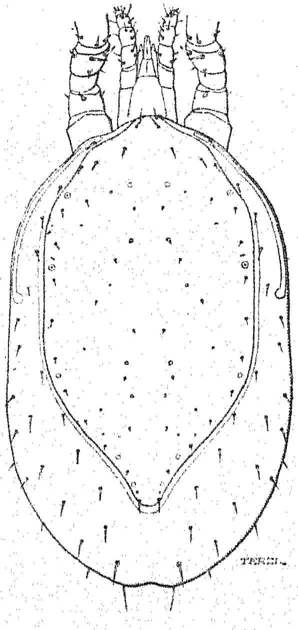
Liponyssus berlesei Hirst, Proc. Zool. Soc. 1921, p. 362.

Canestrini has already described a species of *Leiognathus* = *Liponyssus* from a bat under the name *L. berlesei* (Atti Soc. Ven. Trent. xi. pp. 142–143, 1888), so it is necessary to find a new name for my species from *Myospalax scansus*. I propose the name *L. confucianus* for this species.

LIPONYSSUS MACEDONICUS, sp. n. (Text-figs. 32, 33.)

♀. Differing from *L. sciurinus* etc. principally in the shape of the dorsal shield, which is rather abruptly narrowed at the posterior end so as to practically form a short tail. Hairs on dorsal shield exceedingly minute, a few near the anterior end on the margins being a little longer and the terminal pair at the posterior end of the shield also a little longer than the rest, but still quite short. Hairs on uncovered part of body also short, but two pairs at the posterior end (one of them ventral) are somewhat longer than the others. *Sternal plate* trapezoidal and not short, the posterior margin straight; the three pairs of hairs on this plate are rather short. *Genito-ventral plate* short and fairly wide, its posterior end rounded off. Hairs on venter a little longer than those on the dorsum. *Anal plate* rather elongate pyriform. *Peritreme* reaching almost as far forwards as the anterior margin of the first coxa. Second coxa with the anterior (dorsal) spur large, ventrally this coxa has a large posterior spur (larger than in *L. arcuatus*). Third coxa with two posterior spurs, the inner fairly well developed, the outer weaker. Fourth coxa apparently without any spur. Femur of first leg dorsally with two rather noticeable but not very long spiniform setæ near its distal end and there are also some quite short ones on this limb. Ventrally the tarsus of the second leg has two stout but very short spurs or spinules. Tarsi of third and fourth legs with a spine near the distal end. There are also some weaker spines and setæ on the legs.

Text-figure 32.



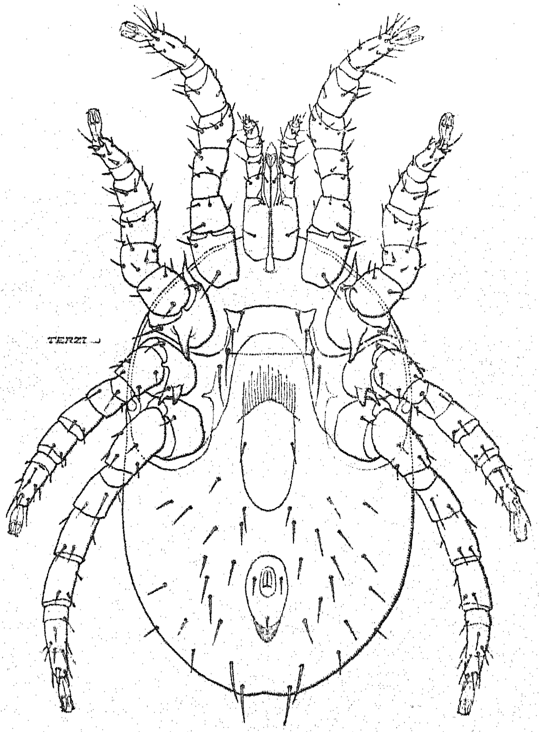
Liponyssus macedonicus, sp. n., ♀. Dorsal view.

♂. *Ventral plate* without any transverse line, it is expanded just behind the last coxæ and afterwards narrows again to form the neck-like portion connecting it with the anal part; the anal part of the plate has a very minute denticle or cone on each of its margins just before the striated tip; there are nineteen hairs on the ventral plate including the posterior unpaired one. *Coxæ* furnished with spurs as in the female, but there is also a slender (outer) spur on the last coxa. Second leg stout but rather short, the fourth leg longer than the others and considerably swollen, one of the spines on the patella and another on the tibia are stouter than the rest. A pair of spinules are present at the distal end of the tarsi of the three posterior pairs of legs.

Length of body (not including capitulum), ♀ ·65–·67 mm.; ♂ ·57 mm.

Host: *Spalax monticola thermaicus*. Doiran, Macedonia. Several specimens collected by Dr. James Waterston (24. x 1918).

Text-figure 33.



Liponyssus macedonicus, sp. n., ♀. Ventral view.

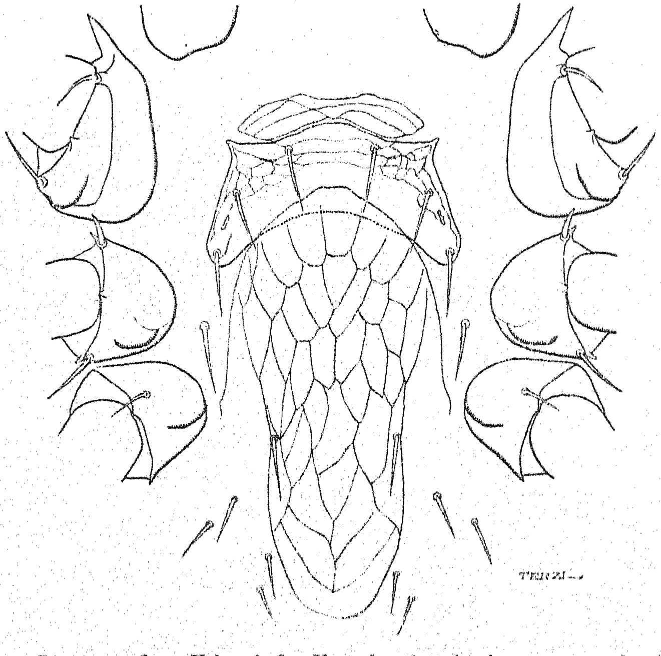
Liponyssus flavus Kolenati. (Text-figs. 34, 35.)

Dermanissus flavus Kolenati, Parasit. Chiropt. 1857, p. 19.

Liponyssus lobatus Oudemans, Tijdschr. Ned. Dierk. Ver. 1904, (2), pp. 18–22, pl. i. figs. 3–17.

♀. A little before the posterior end the *dorsal shield* becomes narrowed, but the tip is not pointed but widely rounded off (almost truncated) as in *L. carnifex*. Hairs on its surface very short and fine; they are not numerous and are distributed as shown in the figure. Hairs on uncovered part of dorsum very numerous, being very short and rather stiff. *Sternal plate* trapezoidal, the posterior margin being strongly concave; the three pairs of hairs on this plate shorter than its length. *Genito-ventral plate* curiously sculptured, especially the anterior part of it (genital operculum) which has scale-like markings; posterior end of this plate rounded off. *Anal plate* more triangular than pear-shaped, the sides being straighter than usual. *Venter* with numerous very short stiff hairs. *Peritreme* reaching as far as middle of the first coxa or a little further forwards. First free segment of *palp* with a large flattened process. Second coxa with the usual strong anterior spur, but without any distinct spurs or tooth-like processes posteriorly; on the outer half of its posterior border, however, it is furnished with a slight but distinct curved raised edge. Third coxa also with a slight curved raised edge posteriorly, the outer half of this coxa is somewhat produced and bears a hair. Fourth coxa with a chitinous line near the posterior margin; sometimes there is a tiny inconspicuous spine connected with an outer series of very minute denticles on the extreme outer side of this coxa, but it is

Text-figure 34.

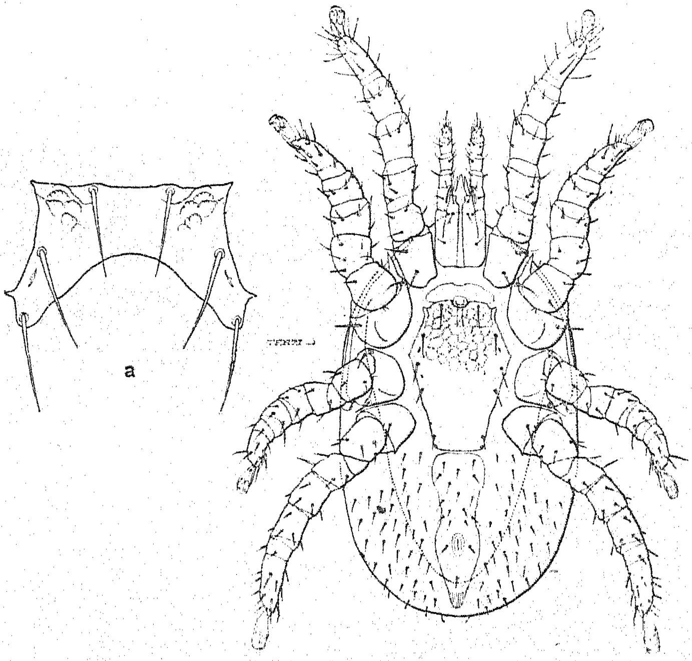


Liponyssus flavus Kolenati, ♀. Ventral surface showing coxæ, sternal and genito-ventral plates.

easily overlooked. There are some rather thick spiniform setæ on the dorsal surface of the legs, those on the femora being especially noticeable.

♂. Posterior end of *dorsal shield* narrowed and angular, being almost pointed, but blunt instead of rounded off as in *L. granulosus. Ventral plate* divided into two regions by a transverse line as in *L. granulosus.* There are five pairs of hairs on the anterior part of this plate and eighteen hairs on the posterior part of it. Hairs on venter numerous and quite short. *Peritreme* apparently somewhat longer than in the male of *L. granulosus*, almost reaching the middle of the first coxa. Fourth leg not specially enlarged.

Text-figure 35.



Liponyssus flavus Kolenati, ♂. Ventral view.
a. Sternal plate of *Liponyssus granulosus* Kolenati, ♀.

Length of body (not including capitulum), ♀ ·65 mm.; ♂ ·54 mm.

Host: Bats. The above description is based on Kolenati's types in our collection labelled *Dermanissus flavus* There are also specimens from a Noctule bat, Aylesford, Kent (27. x. 1919), collected by the author.

LIPONYSSUS GRANULOSUS Kolenati.

Dermanissus granulosus Kolenati, Parasit. Chiropt. 1857, p. 20.

Dermanissus glutinosus Kolenati, ib. p. 20.

♀. Dorsal plate rather like that of *L. flavus* in shape. The hairs on its surface very minute, those on the anterior margin longer, however. *Sternal plate* trapezoidal in shape, the posterior margin strongly concave; in the anterior angle of this plate there are a few rather deep impressions or markings, the rest of its surface being practically smooth and without sculpturing; the three pairs of hairs on this plate are longer than in *L. flavus*, being longer than the plate itself. *Genito-ventral plate* with the markings on its surface very similar to those present in *L. flavus*, the posterior end is rounded off. *Anal plate* pear-shaped, the sides being more convex than in *L. flavus*. *Venter* with numerous short hairs, which are slightly longer than in *L. flavus*. *Peritreme* reaching as far forwards as the middle of the first coxa or slightly further. First free segment of *palp* with a large flattened process as in *L. flavus*. Coxæ of legs very like those of *L. flavus*, the second and third having slight raised curved edges posteriorly, which perhaps represent obsolete spurs.

♂. Posterior end of *dorsal shield* wider and rounded off posteriorly (instead of almost angular and bluntly pointed as in *L. flavus*). Two of the hairs at the posterior end of this shield are much longer than the others. Hairs on uncovered part of dorsum very sparse. *Ventral plate* divided into two regions by a strong transverse line (situate almost opposite the posterior end of the last coxæ). Hairs on the posterior part of this plate less numerous than is the case in *L. flavus* and slightly longer than in that species. There are five pairs of hairs on the anterior part of it as in *L. flavus*, but only 9–10 on the part of it situated behind the transverse line and they are arranged regularly in pairs (whereas there are eighteen on this part of the ventral plate in *L. flavus*). Hairs on venter few in number and slightly longer than those of *L. flavus*. *Peritreme* shorter than in the female, apparently only reaching a little further than the middle of the second coxa. Last pair of legs not enlarged and the bristles and spines are not very stout.

Chelicera furnished with a rather long pointed process besides the two short fingers.

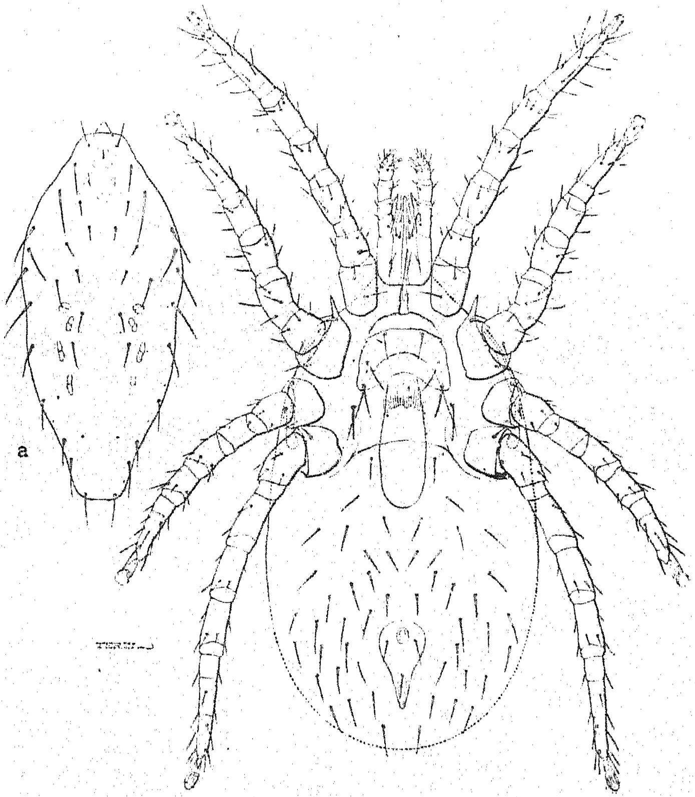
Length of body (not including capitulum), ♀ ·63–·68 mm.; ♂ ·55 mm.

[NOTE.—The male of this species is described from a single example of this sex from the tube labelled *L. glutinosus* by Kolenati, for there were no males in the tube labelled *L. granulosus*.]

Host: Bats. Two tubes (each containing a few specimens) labelled *Dermanissus granulosus* and *Dermanissus glutinosus*. They bear the British Museum Register no. 56.163 (December,

1856) and are described in the register as types presented by Prof. Kolenati. We have also specimens of this species taken on *Vespertilio myotis* at Begamo, ex N. C. Rothschild's collection.

Text-figure 36.



Liponyssus ellipticus Kolenati, ♀. Ventral view.
a. Dorsal shield of same.

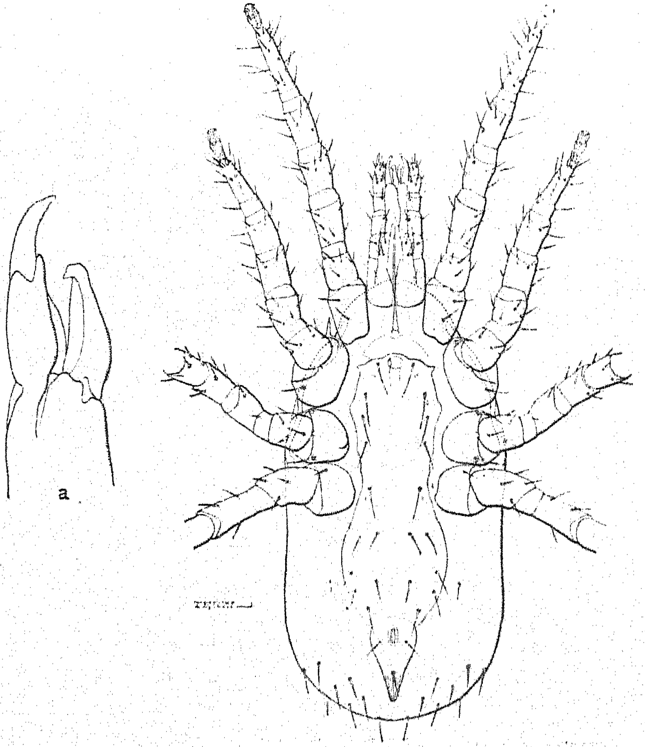
Liponyssus ellipticus Kolenati. (Text-fig. 36.)

Caris elliptica Kolenati, Parasit. Chiropt. p. 16 (1857).

♀. Size large for a *Liponyssus*. *Dorsal shield* more elongated and narrower as compared with its width than that of *L. granulosus* Kolenati, posteriorly it is narrowed, the end being practically truncate; the hairs on the posterior part of the scutum, especially the marginal ones, are much longer than in that species. Hairs on softer uncovered part of dorsum fairly numerous and of moderate length. *Sternal plate* rather large, being longer than that of *L. granulosus*, its posterior margin is concave and not thickened;

the three pairs of hairs on it fairly long. *Genito-ventral plate* with the posterior end rounded off, and it only bears a single pair of hairs. *Anal plate* pear-shaped, the sides of the anterior part of it being well curved, whilst the pointed posterior end is elongated. *Peritreme* rather short. First free segment of *palp* with a process ventrally. Anterior surface of *second coxa* with a long slender spur; except for this one, the coxæ are entirely devoid of spurs or spines. Numerous fine setæ are present on the legs.

Text-figure 37.



Liponyssus longimanus Kolenati, ♂. Ventral view.
a. Chelicera of same.

Length (owing to the damaged condition of the unique specimen it is impossible to give the exact length).

Host: The name of the host is not given on the label, but Kolenati gives it as *Myotis murinus* in the work quoted above.

Liponyssus longimanus Kolenati. (Text-fig. 37.)

Caris longimana Kolenati, Parasit. Chiropt. p. 16 (1857).

♂. *Dorsal shield* with faint reticulate or scale-like markings;

its posterior end is narrowed and practically truncate, the hairs on its surface are not very long, one or two of the marginal ones posteriorly are a little longer, however, and the pair at the end considerably longer than the others. *Ventral plate* with about twenty-five hairs on its surface, including the posterior unpaired one; it becomes greatly enlarged in width behind the last coxæ and is not divided by any transverse line. Hairs on *venter* very few in number and of moderate length (not very long). Movable finger of *chelicera* only about half the length of immovable one. *Peritreme* short, only reaching the second coxa. With the exception of a long slender spur on the anterior surface of the second coxa, the coxæ are without spurs or spines.

Length of body (without capitulum) ·59 mm.

Host: The name of the host is not mentioned on the label, Kolenati says the species is found on *Miniopterus schreibersii* and *Rhinolophus clivosus*.

NOTE.—It seems probable to me that this mite is the male of *Liponyssus ellipticus* Kolenati, but it is better to keep the names separate until proof of this is forthcoming.

Family TARSONEMIDÆ.

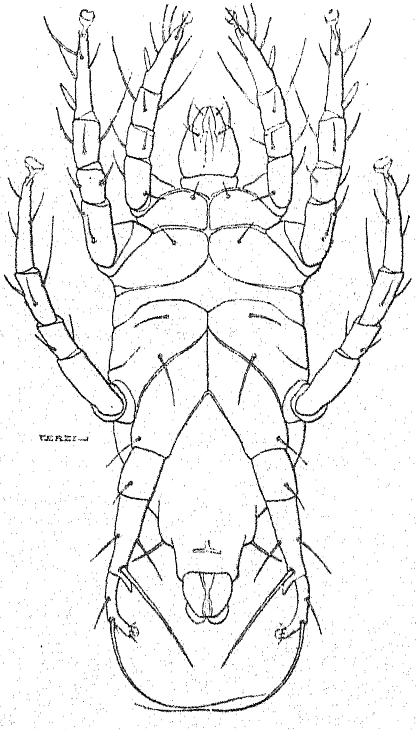
Genus TARSONEMUS Can. & Fanz.

TARSONEMUS TRANSLUCENS Green. (Text-figs. 38, 39, 40.)

♂. *Body* of the male rather long and narrow, being more than twice as long as its greatest width; it is widest at the point at which the posterior pairs of legs are inserted, this part of the abdomen being slightly wider than the cephalothorax. Posterior end of abdomen narrowed and rather tail-like, each of the last segments being considerably narrower than its predecessor. The curious anal structure at the extreme end of the body is only 20 μ wide, the segment preceding it 27–30 μ wide, and the third from the end 40–50 μ wide. When viewed laterally the body is seen to be very high at the level of the posterior legs, but anteriorly it is much lower and the abdomen is narrowed posteriorly as noted above. Hairs on body all rather short. *Legs*. Second leg a little longer than the first and the third is the longest. Fourth leg really the shortest, but its position at the highest and widest part of the body makes it appear longer than the first and second legs: this leg is stouter than the others and its penultimate segment has an angular internal spur or process distally, there is also a long stout bristle situated near it; fourth tarsus curved or bent and a little beyond the middle of its length it is furnished with a very long fine hair, after which the segment becomes slightly reduced in width. Tarsus of the three first legs with a pulvillus, but the terminal segment of the fourth has only a short knob-like structure at the end, it is possible that this is the rudimentary tarsus. There is a stout striated sensory seta on the anterior tarsi, that on the second tarsus being larger than the one on the first. There are also four slender but stiff sensory setæ on the first tarsus.

♀. Body oval, being considerably longer than wide. Hairs on body few in number and quite short and inconspicuous. Pseudostigmata almost circular in shape. First leg the shortest, being slightly shorter than the second. Claw of first tarsus rather large and only slightly curved. The largest of the striated olfactory setæ on this segment is long but slender and situated near the middle, there are also two short striated setæ of the same nature near the proximal end, one of them being club-shaped. In addition to the fairly stout setæ just mentioned there are two pairs of long slender tactile setæ. Second tarsus with a rather long striated seta near its proximal end, but it is a little shorter than the longest of the stout ones on the first tarsus.

Text-figure 38.



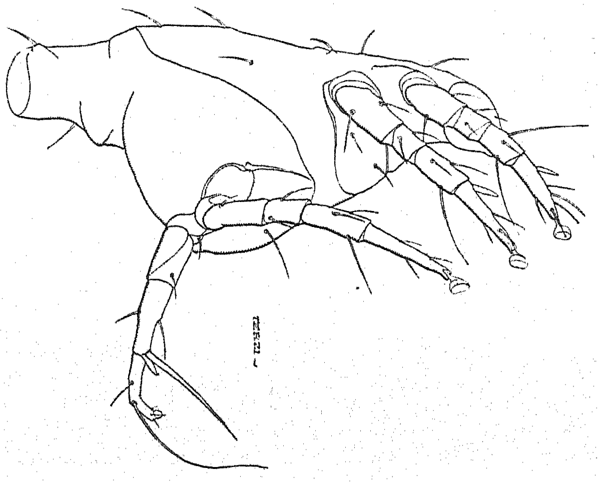
Tarsonemus translucens Green, ♂. Ventral view.

Measurements. ♂. Body (including capitulum) 157–167 μ in length; width of cephalothorax 72–75 μ; greatest width of abdomen about 80 μ. Length of first leg 75 μ, of second 96 μ, of third 122 μ, of fourth (not including the proximal segment) 72 μ.

♀. Body 190–207 μ in length; in width 107–115 μ.

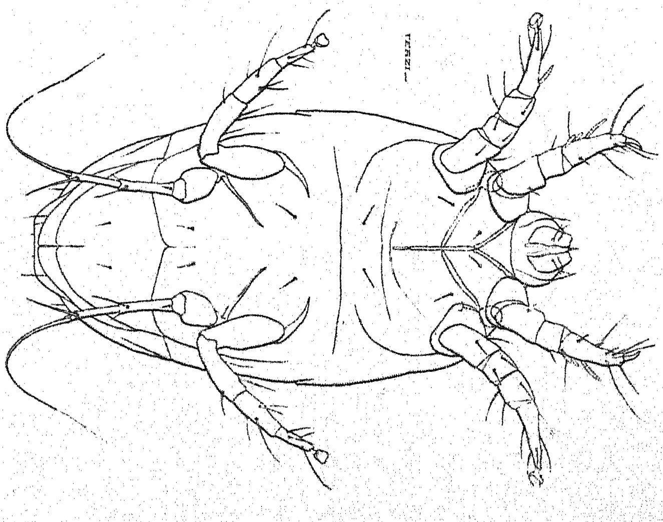
Hab. On *Capsicum*, Trinidad (*F. W. Urich*). On tea, Ceylon (*Hutson*).

Text-figure 39.



Tarsonemus translucens Green, ♂. Lateral view.

Text-figure 40.



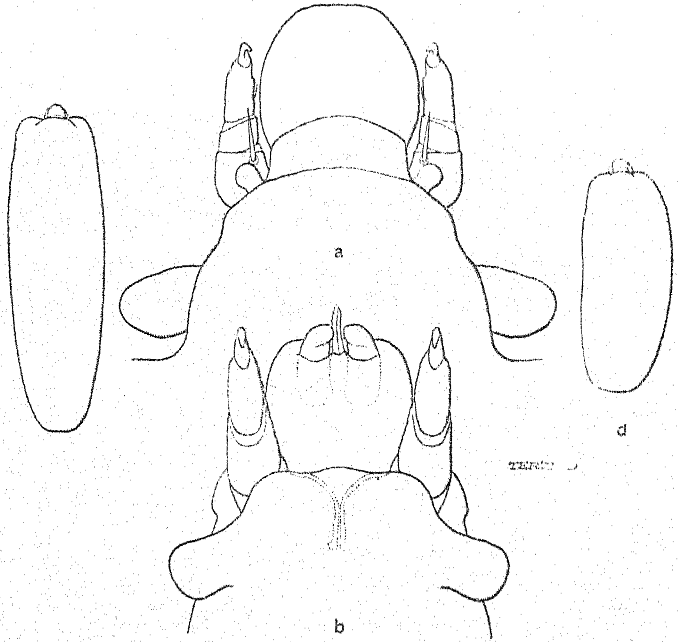
Tarsonemus translucens Green, ♀. Ventral view.

Genus Podapolipus Grassi & Rovelli.

Podapolipus aharonii, sp. n. (Text-fig. 41.)

♀. Body elongated, being from over three to more than three and a half times as long as wide. There are usually a large number of embryos or eggs in the body. Cephalothorax minute and bearing the appendages. Anterior pair of legs minute but segmented, the segments apparently being three in number; a seta is present dorsally at the distal end of the first segment of this leg; the terminal segment has a well-curved hook-like claw at the end. Second pair of legs reduced to smooth little unsegmented sacs. Just above the first leg there is a tiny cone or tubercle at the apex of which is the stigmal orifice. Movable finger of chelicera curved and styliform, being quite slender.

Text-figure 41.



Podapolipus aharonii, sp. n., ♀.

a. Dorsal view of capitulum and anterior end of body showing the legs, etc.
b. The same from below.
c & d. Outline of body of the entire mite showing variation in length.

This species is much more elongated than *P. reconditus* Grassi & Rovelli and *P. grassii* Berl., resembling *P. bacillus* Berl.

(from Java) in this respect, but *Opsomala cylindrica*, the host of the new species described above, is confined to the Mediterranean Region.

Length of body 122–171 μ, its width 40–49 μ.

Host: A number of specimens from the wings of *Opsomala cylindrica* Marsch., Ekron, Palestine, 15. iii. 1921 (*I. Aharoni*).

The specimens were red in colour when alive.

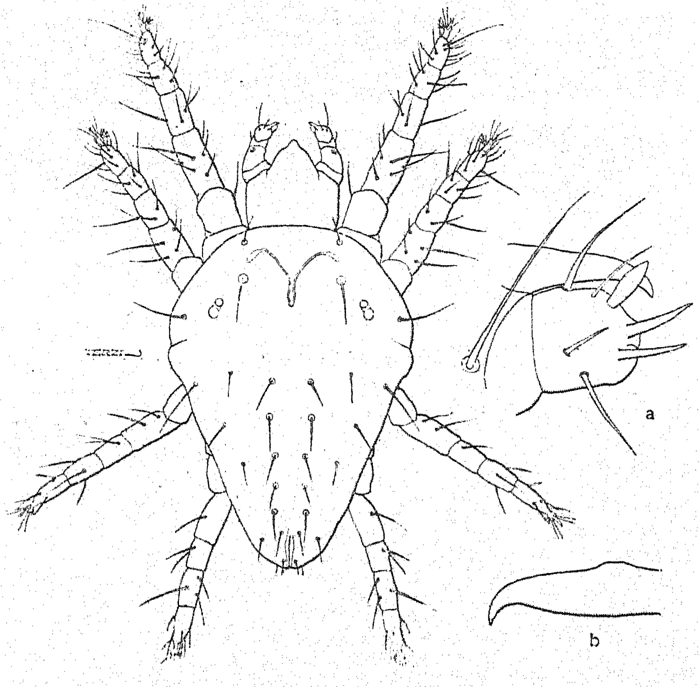
Fam. TETRANYCHIDÆ.

Genus PARATETRANYCHUS Zacher.

PARATETRANYCHUS TRINITATIS, sp. n. (Text-figs. 42, 43.)

♂. Hairs on *body* quite short, they are distributed as shown in the figure, some of them seem plain, but others are furnished with inconspicuous accessory hairlets. Anterior eye distinct although small, the posterior is inconspicuous and easily overlooked, being more weakly chitinised. *Penis* curved at the end

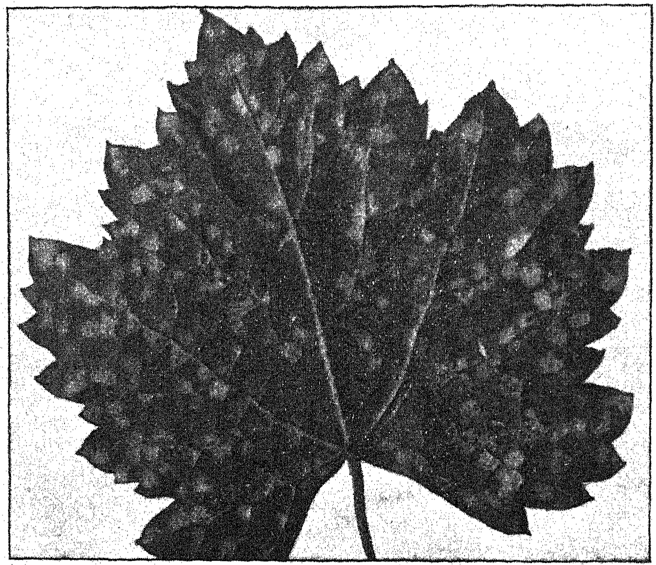
Text-figure 42.



Paratetranychus trinitatis, sp. n., ♂. Dorsal view.
a. Traces of palp. b. Penis from the side, greatly magnified.

and shaped as figured. Dorsal spine on *palp* very short. Dorsal sensory finger stouter than and a little shorter than the two neighbouring rod-like setæ, the latter are of unequal length, one being slightly longer than the other. Terminal sensory finger of palp apparently absent.

Text-figure 43.



Leaf of vine showing discoloration caused by *Paratetranychus trinitatis*, sp. n.

Length of male (including capitulum) 342–375 μ, of hard external part of penis about 11–15 μ, of rod-like setæ of tarsus of palp $4\frac{1}{2}$–6 μ, of dorsal sensory finger of palp $3\frac{1}{2}$–4 μ.

Host plant: Grape vine, Trinidad (*F. W. Urich*).

41. On the External Characters and Classification of the Mustelidæ. By R. I. Pocock, F.R.S., F.Z.S.

[Received June 6, 1921: Read November 8, 1921.]

(Text-figures 27–39.)

Contents.

	Page
Introduction	803
The Rhinarium	805
The Facial Vibrissæ	811
The External Ear	811
The Feet	814
The Anus and External Genitalia	827
The Classification of the Mustelidæ	829

Introduction.

In 1869 Gray (Cat. Carnivorous etc. Mammals Brit. Mus. pp. 79–142) relegated the genera which by all modern zoologists are referred to the family Mustelidæ to two families, Mustelidæ and Melinidæ. The Mustelidæ were divided into the following tribes:—(1) Mustelina for *Martes*, *Mustela*, *Putorius*, *Gulo*, *Galera*, *Grison*; (2) Lutrina for *Lutra* and other genera of typical otters; (3) Enhydrina for *Enhydra*. The Melinidæ were similarly divided into the tribes:—(1) Melina for *Arctonyx*, *Meles*, *Taxidea*, *Mydaus*; (2) Mellivorina for *Mellivora*; (3) Mephitina for *Mephitis*, *Conepatus*, *Spilogale*; (4) Zorillina for *Zorilla* [=*Ictonyx*]; (5) Helictidina for *Helictis*.

From my present standpoint the interest of Gray's classification lies in its influence upon Gill, who in 1872 (Smiths. Misc. Coll. xi. pp. 64–65) followed Flower (P. Z. S. 1869, pp. 11–15) in fusing the Melinidæ and Mustelidæ into one family, for which the latter name was retained, and elevated all Gray's tribes to the rank of subfamilies—Mustelinæ, Melinæ, Zorillinæ, Mephitinæ, etc. As will appear in the sequel, this classification in my opinion better expresses the affinities of the genera dealt with than any that followed it *.

In 1883 Flower (Encycl. Brit., Mammalia, pp. 439–440) divided the Mustelidæ into the following subfamilies:—

(1) Melinæ for *Mephitis*, *Arctonyx*, *Meles*, *Mydaus*, *Taxidea*, *Mellivora*, *Helictis*, *Ictonyx*.
(2) Mustelinæ for *Galictis* [*Tayra* + *Grison*], *Mustela* [=*Martes*], *Putorius* [=*Mustela*], *Gulo*.
(3) Lutrinæ for *Lutra*, *Aonyx*, *Enhydra* [=*Latax*].

This arrangement, based mainly on the structure of the feet, was adopted by Mivart (P. Z. S. 1885, pp. 393–395); and with the addition of *Pæcilogale* and *Lyncodon* to the Mustelinæ was repeated by Flower and Lydekker in 1891 ('Mammalia,' pp. 567–591). It was also accepted by Sedgwick ('Students' Text-Book of Zoology,' ii. p. 624, 1905).

---

* I have intentionally ignored such family names as Mellivoridæ, Zorillidæ, etc., proposed by Rochebrune and Mephitidæ proposed by Rhoads, because no attempt was made to define the families thus casually designated and no reasons were given for assigning that rank to the groups.

In 1902 de Winton ('Zoology of Egypt, Mammalia,' p. 245), trusting apparently to the structure of the teeth, modified Flower's system by transferring *Mephitis*, *Conepatus*, *Mellivora*, and *Ictonyx* from the Melinæ to the Mustelinæ. Max Weber in 1904 (Die Säug. pp. 536–538) followed de Winton with respect to the allocation of *Mellivora*, but otherwise agreed with Flower. And in the same year Trouessart (Cat. Mamm., Suppl. pp. 187–215) also followed Flower, but put *Pæcilogale* into the Melinæ. He further subdivided Mustelinæ into two tribes:—Guloneæ for *Gulo*, *Galictis* [=*Tayra*+*Grison*], and *Lyncodon*, and Musteleæ for *Mustela* [=*Martes*] and *Putorius* [=*Mustela*], with subgenera *Lutreola* and *Arctogale* [=*Mustela*].

In 1912 Miller (Cat. Mamm. Western Europe, pp. 340–341) divided the Mustelidæ into four subfamilies:—(1) Melinæ containing "about a dozen genera," of which only *Meles* is quoted and dealt with; (2) Lutrinæ containing "four genera," *Lutra* alone being discussed; (3) Guloninæ containing *Gulo* and probably *Mellivora*; (4) Mustelinæ restricted to the genera *Martes*, *Mustela* (with its subgenera *Putorius* and *Lutreola* and *Mustela*), and *Vormela* *.

Although Miller, like de Winton, seems to have relied mainly on the teeth, it seems clear that a large number of the genera placed by de Winton in the Mustelinæ were left by Miller in the Melinæ, where Flower placed them. Another point to be noticed in connection with Miller's classification is his severance of *Gulo* from the Mustelinæ as the type of a special subfamily †, with the guess that *Mellivora* is a related genus.

Setting aside for the moment the classifications of Gray and Gill, two conclusions come out from this brief review:—(1) There is complete agreement amongst recent writers with regard to the status of the Lutrinæ; (2) Although Flower's subdivisions have held the field until the present day, there is a great variety of opinion as to the constitution of the Melinæ and Mustelinæ. It is admitted by all that *Meles*, *Arctonyx*, *Taxidea*, *Mydaus*, and *Helictis* are Melinæ; and that *Martes*, *Mustela* (with related generic or subgeneric forms, such as *Vormela*, *Putorius*, *Lutreola*), as well as *Tayra*, *Grison*, and *Lyncodon* are Mustelinæ. But *Mephitis*, *Spilogale*, *Conepatus*, *Mellivora*, *Ictonyx*, and *Pæcilogale* have been placed according to the fancy of authors in either subfamily. It is quite clear therefore that there is something wrong with the classification, and that the characters used for defining the two subfamilies are insufficient for the purpose.

---

* In 1911 Satunin (Mitt. Kauk-Museums, v. p. 267) defined the genera *Vormela* and *Putorius*, admitting the following subgenera of the latter, *Putorius* (s.s.), *Lutreola*, *Ictis*, and *Kolonokus*. The genus *Putorius* is equivalent to *Mustela* as understood by Miller, *Ictis* (=subgenus *Mustela*) being employed for the stoats and weasels. Miller was perhaps not acquainted with this paper when he wrote his 'Catalogue of the Mammals of Western Europe.'

† This was originally done by Gray in 1825 (Ann. Phil. xxvi. p. 339); but in his latest classification he abandoned the group named Guloninæ.

In 1920 (Proc. Zool. Soc. pp. 179–187 and pp. 424–436) I attempted to show that Miller's guess as to the kinship between *Gulo* and *Mellivora* was untenable; and that there is practically no evidence of sufficiently close relationship between *Meles* and *Taxidea* to justify their retention in the same subfamily. *Gulo* was affiliated with *Martes*; Gill's subfamily Mellivorinæ was resuscitated for *Mellivora*; Taxidiinæ was proposed as a new subfamily group for *Taxidea*; and *Meles* and *Arctonyx* were provisionally left as the sole representatives of the Melinæ.

Subsequently (Proc. Zool. Soc. 1921, pp. 473–486 and pp. 535–546) a study of the auditory bullæ in the Mustelidæ supplied additional characters for the definition of the subfamilies; and reasons for the admission of several genera of Lutrinæ were brought forward.

In the following pages the external characters of all available genera, apart from *Gulo*, *Mellivora*, *Meles*, *Taxidea*, and the genera of Lutrinæ, which I dealt with in the papers just mentioned, are described in detail; and a summary of the results setting forth my views on the classification of the Mustelidæ is given at the end.

Most of the material forming the subject-matter of the paper consisted of specimens which had lived in the Zoological Gardens and were examined after death at the Society's Prosectorium. Mr. Oldfield Thomas, however, has given me all the facilities at his command for studying the splendid collection under his charge at the Natural History Museum. I am much indebted to him and to Mr. Martin Hinton for the help received in this way. I am also particularly grateful to Mr. Cyril Hopwood, a member of the Council of the Rangoon Zoological Society, for sending me through Mr. Max Friedlander, the Superintendent of the Gardens, a spirit-specimen of *Melogale personata*; and to Mr. E. Jacobson, for procuring for me at Mr. Boden Kloss's request, a similarly preserved example of *Plesiogale nudipes* * from Fort de Kock on the west coast of Sumatra.

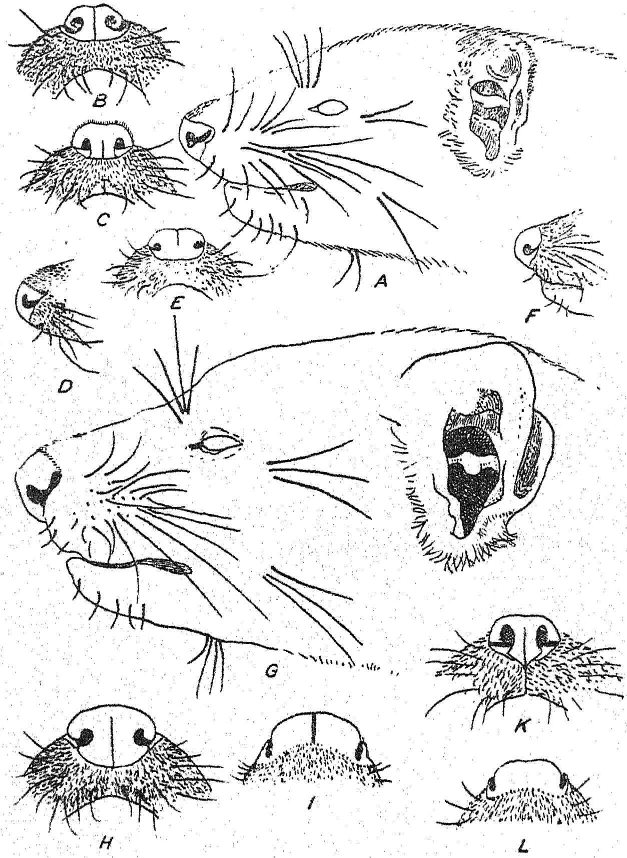
The Rhinarium.

The most primitive type of rhinarium is found in *Martes* and *Gulo*. It is naked above, the lateral slits of the nostrils extend nearly to its posterior margin, the infranarial portions are shallow or moderately deep, the inferior edge is convex or angled, but it is not, strictly speaking, continued over the upper lip—that is to say, the gutter which cleaves the lip consists of smooth skin differentiated by its texture from the rhinarium above. This

---

* Gray referred this species, with others, to his genus *Gymnopus* (see *infra*, p. 818). That name, however, is preoccupied. Hence I propose *Plesiogale* as a substitute.

Text-figure 27.



A. Side view of head of *Putorius putorius*.
B. Front view of rhinarium of the same.
C. The same of *Gale nivalis*.
D. Side view of rhinarium of the same.
E. Front view of rhinarium of *Plesiogale gymnopus*.
F. Side view of rhinarium of the same.
G. Side view of head of *Charronia flavigula*.
H. Front view of rhinarium of the same.
I. Upper view of rhinarium of the same.
K. Front view of rhinarium of *Martes foina*.
L. Upper view of rhinarium of the same.

× $\frac{1}{3}$.

gutter is continued as a groove up the middle line of the rhinarium between the nostrils. (Text-fig. 27, K, L.)

In *Charronia* the gutter is obliterated, except close to the convex lower margin of the rhinarium, which is grooved above, and the upper lip is scantily hairy in the middle line. (Text-fig. 27, G–I.)

In *Gale*, *Mustela*, and *Putorius* it is also obliterated or nearly so, and the infranarial portions of the rhinarium are shallower. In *Gale nivalis* the hair of the muzzle encroaches on the upper surface. (Text-fig. 27, A–D.)

In *Plesiogale nudipes* the rhinarium is large, with a median groove, deep infranarial portions, and naked above back to the posterior ends of the nostril slits. (Text-fig. 27, E, F.)

In *Ictonyx*, as in *Putorius*, the rhinarium is lightly biconvex above and mesially grooved in front, with the inferior edge horizontal in the middle, convex at the sides where it curves backwards; but the infranarial portions are deeper than in *Gale*, *Mustela*, or *Putorius*, and this area of the rhinarium is wider than the upper portion. There is no trace of gutter and the continuously hairy upper lip is about as deep as the height of the rhinarium. (Text-fig. 29, A–B.)

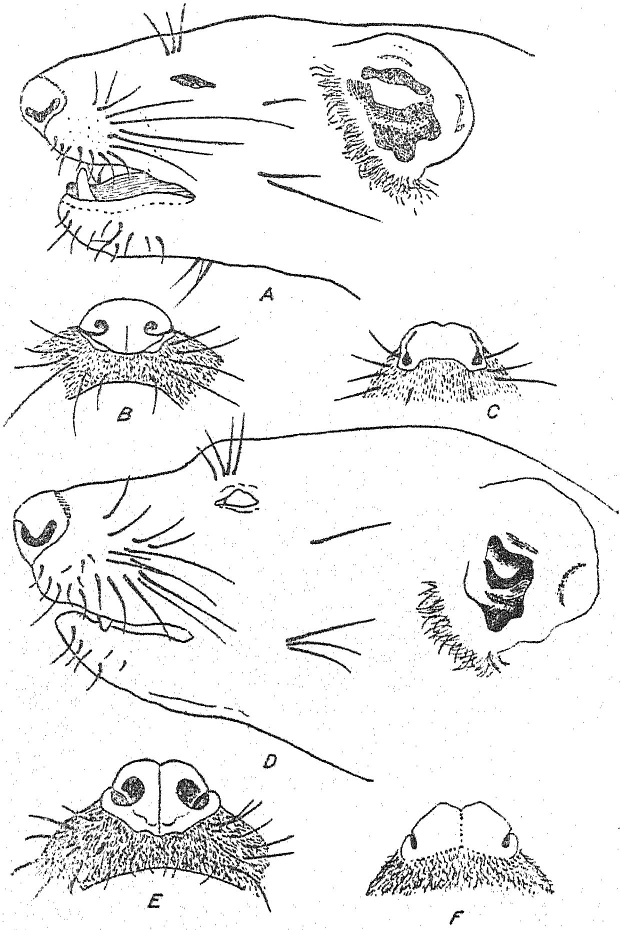
In an example of *Grison furax*, or an allied species, from Brazil, the upper surface of the rhinarium is evenly rounded from side to side, the groove is on the lower half of the front surface, and the nostrils are wide apart. The infranarial portion is deep in the middle, but quite narrow laterally, where it passes beneath the slit of the nostril; and this narrowed piece is defined from the median piece by an oblique groove. There is no trace of gutter and the depth of the lip is less than that of the rhinarium. Two or three specimens of *Grisonella* (sp. ?) from Cordova in the Argentine show individual variation in the rhinarium. In one the upper surface is lightly biconvex, the median groove is distinct, and there is no gutter, in the other the median groove is obsolete, the upper surface is uniformly convex as in *Grison*, and there is a very shallow gutter. In both the infranarial portion is tolerably deep and mesially angled below, but the lateral portions, which in *Grison* pass backwards beneath the nostril slits, are practically obsolete. (Text-fig. 28, A–C.)

In *Tayra barbara* the upper side of the rhinarium is grooved and the anterior surface deeply and widely grooved. The nostrils are larger and closer together than in *Grison* and the infranarial portions are deep both mesially and laterally, and are marked in front, as in *Grison*, by a fine oblique groove on each side which meets its fellow of the opposite side in the middle line above the inferior angle of the rhinarium in front. The rhinarium is about twice as deep as the upper lip, which has no gutter. (Text-fig. 28, D–F.)

The rhinarium of *Taxidea* recalls that of *Gale*, *Mustela*, and *Putorius* in the shallowness of the infranarial portions and the presence of the median groove. It is, however, relatively wider, has the nostrils a little closer together, and the upper surface overgrown with hair nearly to the anterior margin. The lip has no gutter and is not so deep as the rhinarium.

In *Mellivora* the rhinarium is wide as in *Taxidea*, and the

Text-figure 28.



A. Side view of head of *Grison furax* or a closely allied species.
B. Front view of rhinarium of the same.
C. Upper view of the same.
D. Side view of head of *Tayra barbara*.
E. Front view of rhinarium of the same.
F. Upper view of the same.

× ⅓.

upper lip is shallow and without gutter; but the infranarial portions are somewhat deeper than in that genus; there is no median groove and the lateral slits of the nostrils are more abbreviated, and the upper surface is quite naked.

In *Meles* the rhinarium is very large and naked, the infranarial portions being exceedingly deep and often convexly produced in the middle below. The nostrils are tolerably close together, but the lateral slits, although narrow, are long. There is no median groove, and the upper lip, shallower than the rhinarium, has no gutter.

In the Skunks the range in variation of the rhinarium is very instructive. In *Spilogale* it is very like that of *Martes*, having shallow infranarial portions defined by faint grooves from the median portion, a median groove in front in the lower part, an angled inferior border, and a complete gutter dividing the upper lip, which is not quite so deep as the rhinarium. (Text-fig. 29, C.)

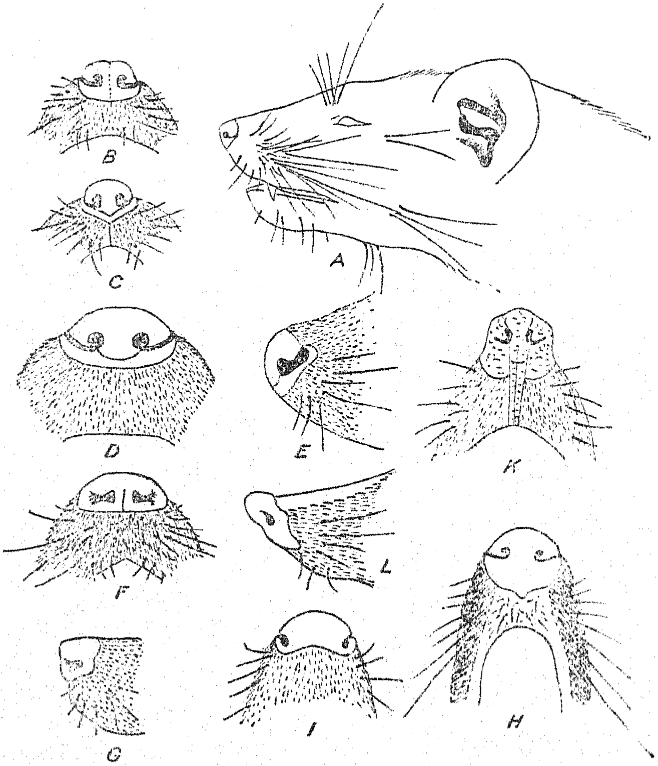
In *Mephitis* the infranarial portions are always deep, wide, and well-defined laterally beneath the posterior slit of the nostrils as in *Meles*, and when the groove between the nostrils and the two defining the infranarial portions and the gutter on the lip are absent, the resemblance to that genus is particularly close. But in a specimen, said to have come from Manitoba, the rhinarium is lower and somewhat wider than in other examples, the lip is cleft by a shallow gutter continued on to the lower half of the rhinarium, and the lateral portions are defined by shallow grooves running from the nostrils to the middle line of the inferior edge. (Text-fig. 29, D, E.)

In *Conepatus proteus* the rhinarium is twice as wide as high, about equal in depth to the upper lip which has no gutter, its upper edge is evenly convex, its lower edge horizontal, and, although there is a short groove between the nostrils, the nostrils themselves are wholly visible from the anterior view, the lateral slits being short and not continued to the posterior edge, thus resembling the rhinarium of *Mellivora*. (Text-fig. 29, F, G.)

In *Melogale personata* the rhinarium is remarkable for the extreme depth of the mesially grooved infranarial portions which are produced inferiorly, so that their median depth is equal to the depth of the area above it and of the upper lip. They are also very deep laterally beneath the slits of the nostrils, which are continued to the posterior border of the rhinarium. The upper lip is ungrooved and is only sparsely hairy mesially and laterally as far back as the angle of the mouth. (Text-figs. 29, H, I; 30, G.)

The rhinarium of *Mydaus* is even more aberrant and recalls that of the Suidæ in the sense that it consists of a somewhat rounded disc with two subcircular nostrils on its anterior surface, the slits of the nostrils being very narrow and short. The infranarial portions are much deeper than the upper portion of the rhinarium and are everywhere of equal depth. They are defined by a vertical groove running downwards from the nostril, and each of these grooves is continuous with the outer edge of a long, narrow, parallel-sided philtrum, of the same texture as the rhinarium, which extends to the edge of the upper lip and is marked by a groove passing upwards on to the rhinarium. In front of the rhinarium above them is a naked strip of skin on the muzzle. (Text-fig. 29, K, L.)

Text-figure 29.



A. Side view of head of *Ictonyx capensis.*
B. Front view of rhinarium of the same.
C. The same of *Spilogale putorius.*
D. The same of *Mephitis mephitica.*
E. Side view of the same.
F. Front view of rhinarium of *Conepatus proteus.*
G. Side view of the same.
H. Front view of rhinarium of *Melogale personata.*
I. Side view of the same.
K. Front view of rhinarium of *Mydaus meliceps* (from dried skin).
L. Side view of the same.

× ⅓.

The genera may be grouped as follows by the rhinarium :—

- *a*. No complete and true philtrum resembling the rest of the rhinarium in texture dividing the upper lip, which is at most grooved.
  - *b*. Upper lip divided by a complete groove of smooth naked skin, giving mobility to the right and left halves .... *Gulo*, *Martes*.
  - *b′*. Groove on upper lip obliterated or nearly so, the two halves of the lip not separately movable, or only slightly so.
    - *c*. Infranarial portion of rhinarium much shallower beneath lateral slits of nostrils than above them.
      - *d*. Infranarial portion laterally very narrow...... *Mustela*, *Gale*, *Putorius*, *Charronia*, *Grison*, *Taxidea*.
      - *d′*. Infranarial portion laterally moderately deep... *Tayra*, *Ictonyx*, *Spilogale*, *Mephitis*, *Conepatus*.
    - *c′*. Infranarial portion very deep beneath lateral slits, approximately as deep as portion above them .... *Meles*, *Melogale*.
- *a′*. A long narrow philtrum, resembling the rest of the rhinarium, dividing the upper lip; infranarial portions everywhere very deep.. *Mydaus*.

The Facial Vibrissæ.

The number of tufts of facial vibrissæ characteristic of the Carnivora is typically present in the Mustelidæ; but the vibrissæ themselves are longer and more numerous in predatory forms (like *Martes*, *Mustela*, and *Ictonyx*) than in fossorial forms (like *Mellivora*, *Meles*, and *Mephitis*). They are especially well developed in the matter of rigidity and number in the truly semi-aquatic genera like *Lutra* and *Amblonyx*; but in the tropical West-African Otter, *Paraonyx*, Hinton records the complete absence of the superciliary and upper genal tufts. In other genera, like *Meles*, the upper genal tuft is sometimes apparently absent; but a noticeable point about this tuft in all genera, when it is present, is its high position on the cheek, only a little below and behind the posterior corner of the eye. In the one fresh example of *Tayra barbara* examined, I could find no trace of the interramal tuft. (Text-figs. 27–29.)

In *Melogale personata* the vibrissæ are all long and numerous as in predatory forms, the submentals being unusually well developed on the area of nearly naked skin which runs along the lower lip as far as the angle of the mouth, corresponding to that of the upper lip. (Text-fig. 30, G.)

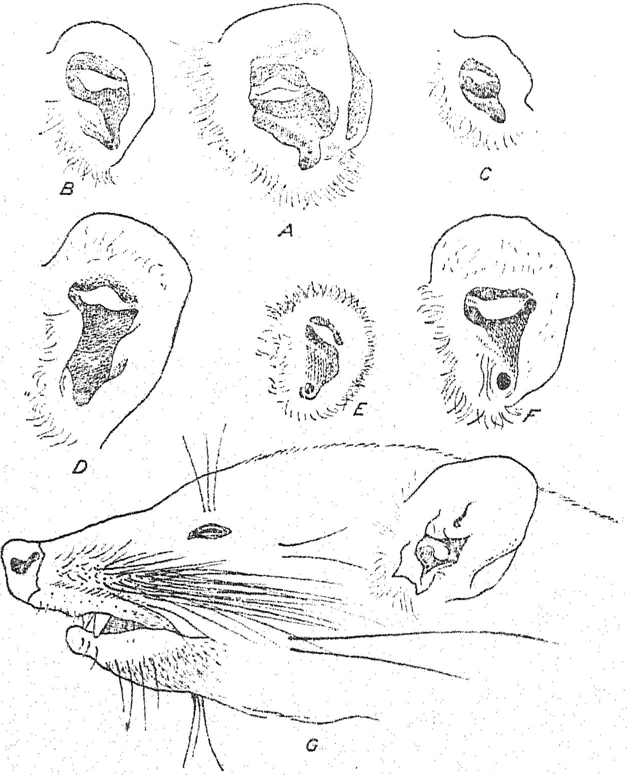
The External Ear.

The external ear shows every grade between high specialisation, the primitive condition, and almost complete degeneration. In its highest types, as exemplified by *Martes* * and *Charronia*, it is of tolerably large size and is provided with a well-developed bursa, the posterior flap of which is large, has a strongly convex margin, and is attached above behind the straight-edged portion of the posterior border of the ear which constitutes the anterior flap. The supratragus has a simple subglobular thickening. The tragus and supratragus are well defined and separated by a distinct notch, and the antero-internal and postero-internal thickenings descend behind or within the tragal and antitragal prominences respectively. (Text-fig. 27, G.)

---

* See my paper on the Pine and Beech-Martens (P. Z. S. 1914, pp. 1062–1068).

Text-figure 30.



A. Ear of *Gale nivalis*.
B. „ *Pœcilogale albinucha* (from dried skin).
C. „ *Lyncodon patagonicus* („ „).
D. „ *Mephitis mephitica*.
E. „ *Conepatus proteus*.
F. „ *Spilogale putorius*.
G. Side view of head of *Melogale personata*.

D, E, F, G, $\times \frac{1}{3}$.

In *Mustela*, *Gale*, *Plesiogale*, and *Putorius* the ear is relatively smaller and rounder than in *Martes*, and further differs in that the thickening of the supratragus is larger and valvular, and the edge of the cavity has a small soft membranous flap just above the supratragus, which is especially well developed in *Plesiogale*. Moreover, the antero-internal thickening curves sharply beneath the supratragus posteriorly. In *Gale*, *Mustela*, and *Plesiogale* the bursa is almost or quite as well developed as in *Martes*, but in *Putorius* it is reduced to a marginal slit, owing to the reduction in size of the posterior flap, the edge of which is nearly straight. (Text-figs. 27, A; 30, A.)

Gulo has the pinna like that of *Martes*, but relatively smaller and provided with a smaller bursa; and the pinna of *Melogale* is very like that of *Mustela* and *Gale*, the bursa, tragus, and antitragus being well developed, but the supratragus is less valvular, the antero-internal ridge descends more vertically, and there is a little pouch above the hollow. (Text-fig. 30, G.)

Tayra and *Grison* also resemble *Mustela* and *Gale* in the presence of the upper membranous flap, the valvular supratragus, the posterior curvature of the antero-internal ridge beneath the supratragus; but differ in the reduction of the bursa to an even greater extent than is seen in *Putorius*. The posterior flap is continuous above and below with the margin of the pinna, and the anterior flap is represented by a very shallow ridge of integument a little in front of it, so that the pouch is reduced to a minimum. In *Grison* and *Grisonella* the valvular supratragus and the flap above it are larger than in *Tayra*; and in *Grisonella* the anterior ridge of the bursa is shorter than in *Grison*. (Text-fig. 28, A, D.)

In *Ictonyx*, and also in *Pœcilictis* and *Pœcilogale*, judging from dried skins, the pinna differs essentially from that of *Mustela*, *Gale*, and *Putorius* in the total absence of all trace of the bursa and of the membranous flap above the supratragus. Otherwise it is similar. (Text-figs. 29, A; 30, B.)

In *Meles* and *Taxidea* the pinna is smaller than in *Ictonyx*, and the supratragus has a simple subglobular thickening as in *Martes*. Otherwise they are tolerably similar; the pinna is less salient in *Taxidea* than in *Meles*.

In *Lutra* the pinna, although much reduced, is of the same simple type as in *Meles*. In *Hydrictis* it is simplified by the almost complete suppression of the tragus and antitragus and of the supratragus apart from the subglobular thickening.

In *Spilogale*, *Mephitis*, and *Conepatus* a noticeable peculiarity in the pinna is the entire absence of the tragal thickening, so that the external orifice of the ear is exposed and not hidden in a cup-like hollow; and the cavity of the pinna has no definite anterior rim. The low antero-internal ridge curves posteriorly beneath the valvular supratragus, which appears to be set higher in the ear than in other genera. The pinna is of comparatively large size in *Spilogale*; but in *Conepatus*—at all events, in *C. proteus*—it is much reduced and scarcely stands away from the head. There is no trace of the bursa. (Text-fig. 30, D–F.)

In *Lyncodon* also the pinna is as much reduced as in *Conepatus*, standing away from the head as a shallow short ridge, the lower end of which does not reach nearly to the *aditus inferior*. There is no bursa, but the structure of the ridges could not be determined on dried skins. (Text-fig. 30, C.)

The pinna of *Mellivora* surpasses even that of *Conepatus* and *Lyncodon* in reduction in size. It is represented merely by a thickening of the integument, without any free edge, round the small cavity; and, judging from the descriptions, the pinna of *Mydaus* is very similar to that of *Mellivora*, but I am unable to say whether the orifice is exposed as in *Mephitis*, *Spilogale*, and *Conepatus* or concealed by a tragal thickening.

The following table shows briefly the principal modifications in the external ear:—

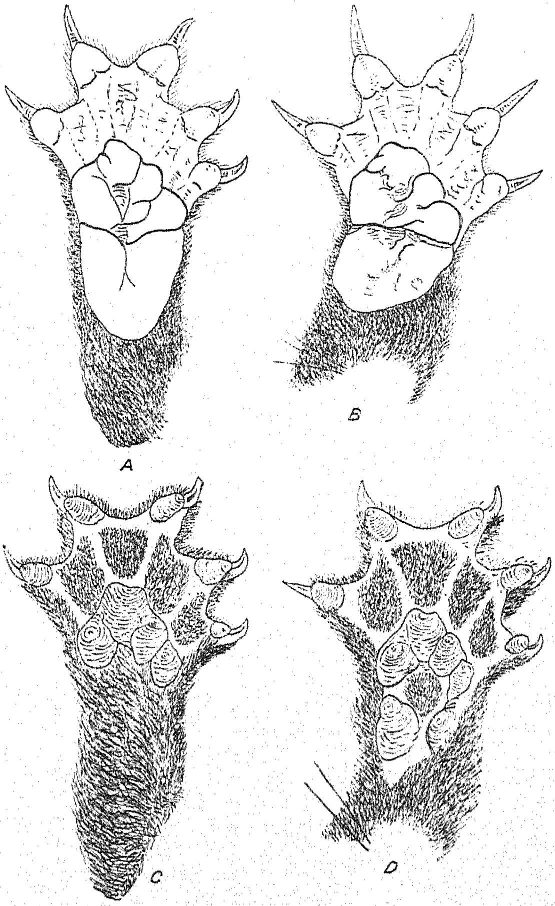
a. Bursa retained.
b. Bursa marginal, upper end of its posterior flap hidden by that of anterior flap .... *Mustela*, *Gale*, *Plesiogale*, *Putorius*, *Martes*, *Charronia*, *Gulo*, *Melogale*.
b′. Bursa remote from margin, shallow, its posterior flap in no way concealed by anterior flap................ *Tayra*, *Grison*, *Grisonella*.
a′. Bursa absent.
c. Auditory orifice concealed, usually by tragal thickening.
d. Pinna laminate, standing away from head.
e. Supratragus a well-developed valvular flap .... *Ictonyx*, *Pœcilictis*, *Pœcilogale*.
e′. Supratragus at most a ridge with rounded thickening.
f. Pinna moderately large .... *Meles*, *Taxidea*.
f′. Pinna much reduced .... *Lutra*, *Amblonyx*, etc.
d′. Pinna a thickened rim of integument .... *Mellivora*.
c′. Auditory orifice exposed, not concealed by tragal thickening .... *Spilogale*, *Mephitis*, *Conepatus*.

The Feet.

In describing the feet of the Mustelidæ I start with two assumptions. First, that the primitive feet were adapted for running or climbing, or both combined, and not for digging or swimming, which hamper, if they do not prevent, the first-mentioned activities. Second, that the feet were naked below, provided with short curved claws, interdigital webbing up to the proximal end of the pads, large 4-lobed plantar pads, double carpal and metatarsal pads, and a hairy heel; and that the digits were unequal in length, the first being the shortest, the second and fifth next and approximately equal in length, and the third and fourth the longest and also approximately equal, so that the digital pads, when not spread, formed a strongly curved line round the anterior margin of the plantar pad. And possibly in the hind foot the third and fourth digits were more closely tied together than to the second and fifth respectively.

The genera whose feet most nearly approach these hypothetical feet are *Tayra* and *Grison*. It is therefore needless to describe them in detail. From the material examined I have not been able to satisfy myself that there is any fundamental difference between the feet of the two, unless it be that in *Grison* the plantar pads are defined from the carpal and metatarsal pads by a deeper and wider groove. In *Tayra* these pads are confluent throughout their width, there is only a very slight trace of division between the two moieties of the carpal pad and none in

Text-figure 31.



A. Right hind foot of *Tayra barbara*.
B. Right fore foot of the same.
C. Right hind foot of *Charronia flavigula*.
D. Right fore foot of the same.

× ½.

the case of the metatarsal pad [*]. In an example of *Grison furax* or an allied form, from Brazil, there is a comparatively large area between the plantar and carpal pads, the latter are well defined but mesially in contact, and there is some naked skin above the large external pad. Similarly, in the hind foot there is some naked skin above the somewhat rounded metatarsal pad, which except internally is distinctly separated from the plantar pad. These differences from the feet of *Tayra* are, however, not so well defined in examples of *Grisonella* from Cordova in the Argentine. In both genera the pads are granular and tessellated, and the third and fourth digits of the hind foot are a little nearer together than they are respectively to the second and fifth. Nevertheless, there is quite a marked extent of web between their pads. (Text-figs. 31, A, B; 32, C, D.)

Of these two genera *Tayra* is an active tree-climber like *Martes*, and *Grison* an agile ground-hunter like *Mustela*; and in *Martes* and *Mustela* and genera related to them the highest type of feet subservient to those modes of life are found. The claws are shorter and more curved, the digits are more widely separable, and the third and fourth of the hind foot are not closer together than to the second and fifth respectively. The underside of the webs is more or less hairy, there is at least a patch of hair between the carpal and plantar pads, the carpal pads are quite separated, the metatarsal pad is absent, the hair of the calcaneum extending down to the plantar pad, and all the pads are narrower and transversely or concentrically ridged and grooved.

Of the genera related to *Martes*, *Charronia* [†] has feet which depart least from the type seen in *Grison* and *Tayra*, although still very distinct. The area between the digital and plantar pads has four large patches of hair on the interdigital webs; but these do not reach the edge of the webs distally or the plantar pads proximally, and the lower side of the digits is also naked; and there is a similar patch of hair surrounded by naked skin on the area between the carpal and plantar pads, which are well developed, the pollical and hallucal elements of the latter being widely confluent with the plantar, while the internal and external moieties of the carpal pads are large and have a small area of naked skin above them. (Text-fig. 31, C, D.)

In *Martes martes* and *M. foina* the area between the digital and plantar pads is covered with hair, except for narrow naked strips radiating along the digits; the area between the plantar and carpal pads and round the latter is also continuously hairy;

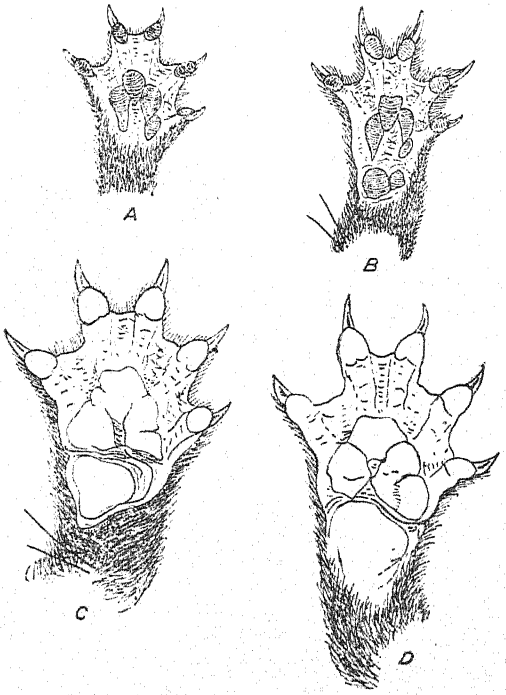
---

[*] Lönnberg (Arkiv för Zool. viii. no. 16, p. 10, 1913) figured the hind feet of two forms of *Tayra* from different altitudes and localities in Ecuador, to show that the combined plantar and metatarsal pad—there being no line of demarcation between them—is longer in the race from the lowlands. Defects in the drawings of these feet may be attributed to their being taken from skins softened in water after being dried.

[†] In 1918 I resuscitated this genus of Gray's, based upon *Martes flavigula*, when I found that the baculum differs greatly from that of *Martes martes* and *M. foina* (Ann. & Mag. Nat. Hist. (9) i. pp. 308–310).

the plantar pads are smaller, more subdivided, their pollical and hallucal elements are connected by a narrow strip with the main pad, and the carpal pads are much reduced and separated by a longer space from the plantar pad. *M. foina*, however, has much larger digital, plantar, and carpal pads than *M. martes**, and thus more nearly approaches *Charronia*. In *M. martes* the digital pads are narrowly ovate, the plantar pads are broken up into four areas connected by narrow naked strips, and the carpals are quite small.

Text-figure 32.



A. Right hind foot of *Pœcilogale albinucha* (from dried skin).
B. Right fore foot of the same.
C. Right fore foot of *Grisonella* sp. from Cordova, Argentine.
D. Right hind foot of the same.

In *Mustela erminea* and *hibernica*, *Gale*† *nivalis* and *africana*, *Putorius putorius*, *furo*, and *nigripes* the feet, except that they are relatively shorter and stouter, generally resemble those of

---

* For figures illustrating these differences, subsequently verified on other specimens, see my paper on these species of *Martes* (Proc. Zool. Soc. 1914, pp. 1062–1068).

† Distinguishable from *Mustela* by the shape of the baculum.

Martes in hairiness and pad development. But in *G. africana* alone have I found the plantar pad broken up into four elements to the same extent as in *M. martes*; and only in *G. africana* could I find the inner moiety of the carpal pad; but, judging from its minute size in this species, it may have been overlooked in the others. (Text-fig. 33, C–F.)

Writing of the Minks (*Lutreola*), Flower and Lydekker ('Mammals, Living and Extinct,' p. 586), said that they differ from the Polecats, Stoats, and Weasels "by the toes being partially webbed and by the absence of hair in the intervals between the naked pads of the soles of the feet." From this statement it seems quite clear that neither of these authors was aware that the toes of Polecats, Stoats, and Weasels are fully webbed up to the digital pads. As for the hairiness of the soles of the feet, I cannot discover from examining the long series of dried skins of Minks in the British Museum that there is any essential difference between them and Polecats, Weasels, and Stoats in that or any other particular. The area between the plantar and digital pads is covered with hair; and it appears that Baird was perfectly correct when he said that the feet are well furred between the pads, though the hair is scantier in summer than in winter.

In some members of this group, however, the feet are quite naked beneath. Gray, for example, based the genus *Gymnopus* * upon certain Oriental species related to *Mustela* and *Gale*, namely *nudipes*, *strigidorsa*, and *kathiah*; and to these *africana* was added. According to the diagnosis the soles of the hind feet in these species have three oblong pads, an arched and bald space behind them, and the heel hairy. But in the Egyptian example of *Gale africana* above referred to the feet are approximately as hairy as in *G. nivalis*; and in *kathiah*, which I provisionally retain in *Mustela*, pending the discovery of the structure of the baculum or other characters to settle its affinities, there is a patch of hairs on the lower side of the webs and also between the carpal and plantar pads, and the hair extends down to the plantar pad on the hind foot. Thus both *africana* and *kathiah* fall outside the genus according to the diagnosis.

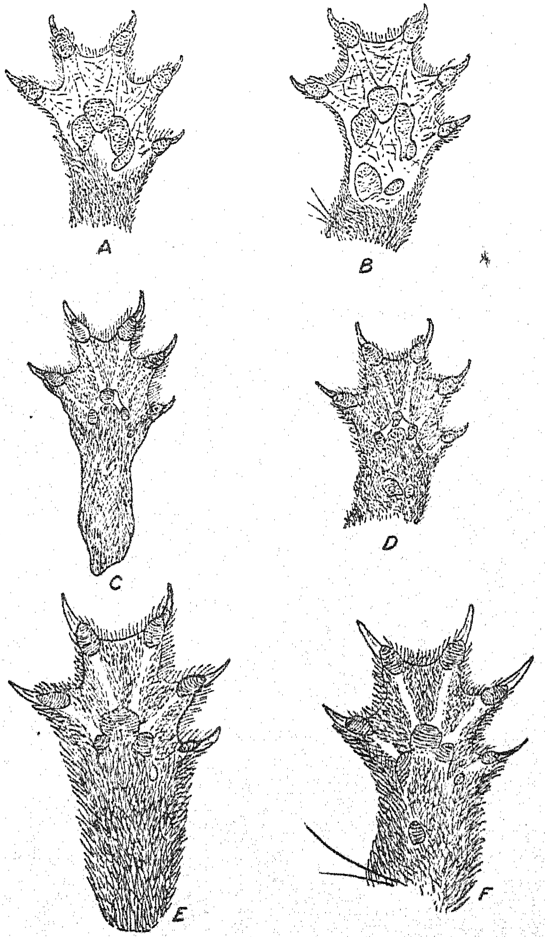
In *Plesiogale nudipes* and *strigidorsa* the feet are quite naked beneath, and the plantar and carpal pads are relatively considerably larger than in *Mustela*, *Gale*, and *Putorius*, and apparently less coarsely striated. The plantar pads are very distinctly four-lobed, the three main lobes being widely in contact, while the pollical and hallucal lobes are attached to the posterior end of the inner of the three main lobes. The two carpal pads are well developed and almost in contact. Just above them there is a narrow naked space, and there is a corresponding space, which, however, seems to vary individually in *P. nudipes*, and lies behind the plantar pad of the hind foot. (Text-fig. 33, A, B.)

---

* Quoted in this paper as *Plesiogale* (see above p. 805), of which *nudipes* is the type-species. I premise that the group is at least as much worth nominal recognition as *Lutreola* or *Kolonokus*.

The feet of these two species are of great interest. It might be claimed that their nakedness is a secondarily acquired character, correlated with life in warmer latitudes than those

Text-figure 33.



A. Right hind foot of *Plesiogale nudipes*.
B. Right fore foot of the same.
C. Right hind foot of *Gale nivalis*.
D. Right fore foot of the same.
E. Right hind foot of *Putorius putorius*.
F. Right fore foot of the same.

frequented by typical Stoats, Weasels, and Polecats. If *nudipes*, which ranges from the Malay Peninsula to Borneo, were alone concerned, that view would be more defensible than, in my opinion, it is. But *strigidorsa* occurs much farther to the north, in Sikhim. Again, it must be remembered that the tropical American species *brasiliensis*, which may be taken as the type of Gray's genus *Neogale*, if it be resuscitated, has hairy feet. I incline, therefore, to the opinion that in *Plesiogale* we have the most primitive type of foot met with in the subfamily Mustelinæ as here restricted—a foot which differs mainly from that of *Grison* and *Grisonella* in the complete suppression of the metatarsal pads.

The feet of *Gulo* * resemble in all essential respects those of *Martes*, except that they are relatively broader.

The feet of *Pœcilogale* are very like those of *Plesiogale*, but the claws of the fore feet are a little larger and the third and fourth digits of the hind foot less widely separated. In both these particulars *Pœcilogale*, so far as the feet are concerned, connects *Plesiogale* with *Ictonyx*, which in the length of the claws belongs to the fossorial group of Mustelidæ—*Pœcilogale* being one of those genera in which the distinction between fossorial and cursorial Mustelidæ breaks down. (Text-fig. 32, A, B.)

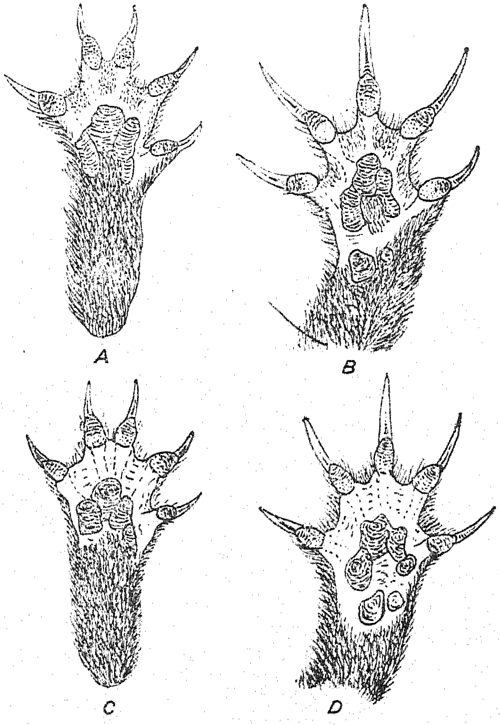
In the remaining genera the feet are fossorial and characterised by long and blunt claws, which are especially long on the fore feet. The only other point they have in common is close union, sometimes amounting to basal fusion, between the digital pads of the third and fourth digits of the hind feet—a phenomenon foreshadowed in the feet of *Grison* and *Tayra* and *Pœcilogale*.

Fossorial feet which come nearest to the feet of the Weasels, Polecats, and Martens, although differing in the characters mentioned in the last paragraph, are found in *Ictonyx* and *Pœcilictis*. The feet, closely resembling those of *Pœcilogale*, are tolerably narrow, and the digits, apart from the third and fourth of the hind foot which are close together, are widely separable; the metatarsal area is without trace of pads and covered with hair down to or nearly down to the plantar pad; the digital pads are oval, well defined, and coarsely striate—at least apically; the plantar pad is narrow, deeply emarginate behind, and very distinctly four-lobed, and the lobes are coarsely striate and are in contact to about the same extent as in *Martes foina*; there are two striate carpal pads, a smaller inner and a larger outer, separated from each other and from the plantar pad by about the same distances as in *Martes foina*, although the sizes of these pads and the distances above mentioned vary according to the species. The carpal pads are largest and the distances in question smallest in the species in which the area round them and the area between the plantar and digital pads are naked. In other species the hair of the carpus extends to the carpal pads, overlaps the inner and spreads into the posterior emargination of the plantar pad; and there is a scanty patch of hair upon the lower side of the interdigital integument*. (Text-fig. 34, A–D.)

---

* See my paper on the external characters of this genus (Proc. Zool. Soc. 1920, pp. 179–187).

Text-figure 34.



A. Right fore foot of *Ictonyx capensis*, from S. Africa, with hair on interdigital integument.
B. Right fore foot of the same.
C. Right hind foot of *Ictonyx* sp., from the Sudan, with naked soles.
D. Right fore foot of the same.

× $\frac{1}{3}$.

In *Pœcilictis* the feet are more like those of typical *Mustela*, in the sense that the soles are much more thickly hairy and the plantar pad is smaller and more subdivided, no doubt in conformity with the sandy habitat of the animal.

The feet of *Taxidea* resemble those of *Ictonyx* in the absence of the metatarsal pad, but in most respects they are very different. The digits are shorter, closer together, with the pads larger, less well defined, and the interdigital webs (although narrower) extend further up the pads, especially on the fore foot. The plantar pad of the broad fore foot, although wider than long, is narrower than the foot itself, indistinctly lobate, and much less deeply emarginate behind; there is a single small carpal pad, representing the outer * of the normal two, set a little distance behind the plantar, and the area behind this and the plantar pad is partially overgrown and overlapped by hairs on the inner or pollical side of the foot as in some examples of *Ictonyx*. In the hind foot the plantar pad is longer than wide, narrower than the foot, irregularly heart-shaped, and very indistinctly subdivided. The pads are granularly roughened.

---

* Thus Thomas's statement that *Ictonyx* may be distinguished from *Pœcilictis* by the nakedness of the soles of the feet does not hold good.

The feet of *Lyncodon*, judging from dried skins, are peculiar in the almost complete suppression of the interdigital webs, which extend only a short distance beyond the plantar pads. The underside of the digits and the area between the digital and plantar pads is naked, but the sides of the digits are fringed with longish hairs. In the fore foot the claws are long and fossorial, the plantar pad is strongly arcuate and short, the hairs of the carpus encroaching upon it in the middle line behind. The carpal pad is represented only by the outer moiety, which is continuous distally with the outer lobe of the plantar pad. The carpal vibrissæ are retained, although the claws are fossorial.

The hind foot closely resembles the fore foot, but the claws are short; and there is no trace of metatarsal pads, the metatarsus being covered with hair, which extends over the middle of the plantar pad. (Text-fig. 35, A, B.)

In all the other genera of fossorial footed Mustelidæ the metatarsal pad is retained and is of large or comparatively large size.

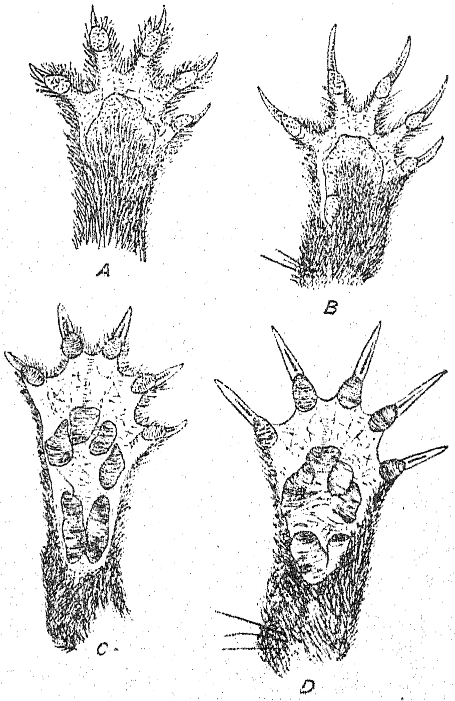
In *Melogale personata* † the fore foot is a little wider than the hind foot, the digits are webbed to the proximal ends of the well-defined digital pads, the soles are entirely naked as far back as the proximal ends of the carpal and metatarsal pads, and all the pads are tolerably coarsely striated, although less coarsely than in *Mustela*, *Martes*, *Gulo*, and *Ictonyx*. The fore foot otherwise tolerably closely resembles that of *Meles*, but the digits are rather more separable, the digital pads are better defined, the plantar pad is relatively narrower, more distinctly four-lobed, with its anterior and posterior margins more curved, the two elements of the carpal pad are in contact or very nearly so in the middle line, and the carpal vibrissæ are well developed. In the hind foot the digits are markedly more widely separable than in *Meles*, there being quite a distinct space between the third and fourth, although the space is narrower than that between the second and third or fourth and fifth. As in the fore foot the digital pads are better defined, the plantar pad is narrower, much more strongly curved, and very distinctly four-lobed, the hallucal lobe, like the pollical lobe of the fore foot, being as large as the others individually. There are two well-defined elongated metatarsal pads, confluent in the middle line proximally, and the hairy calcaneal area is a little shorter relatively than in *Meles meles*. (Text-fig. 35, C, D.)

---

* In my paper on *Taxidea* and *Meles* (Proc. Zool. Soc. 1920, p. 428) I inadvertently described the carpal pad as representing the inner or radial carpal of *Meles*.

† Hodgson figured the hind foot of this species, but wrongly labelled it *Urva cancrivora* (Journ. As. Soc. Bengal, xvi. pl. ii.). A figure of the fore foot is in his unpublished drawings.

Text-figure 35.

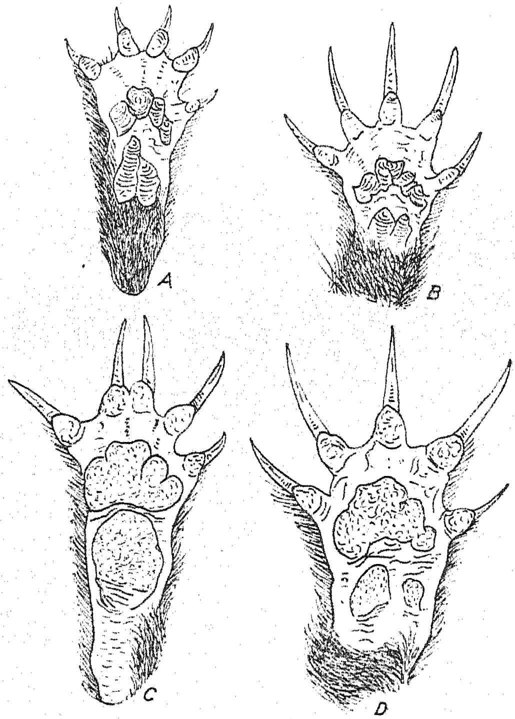


A. Right hind foot of *Lyncodon patagonicus* (from dried skin).
B. Right fore foot of the same.
C. Right hind foot of *Melogale personata*.
D. Right fore foot of the same.

C, D, × $\frac{1}{3}$.

The feet of *Meles meles* I have already described and figured (Proc. Zool. Soc. 1920, pp. 426–428, fig. 20, A, B). In addition to the differences mentioned above, it may be added that they are of a more decidedly fossorial type than in *Melogale*, the hind foot being narrower as compared with the fore foot, with the pads of the third and fourth digits confluent. In both the fore and hind foot the plantar pads are very wide, the carpal pads of the fore foot are separated, and there is a patch of hair on the area behind the plantar pad. In the hind foot the metatarsal pads are shorter and more confluent, and closer to the plantar pad than in *Melogale*, and all the pads are granular or papillate, not striated.

Text-figure 36.



A. Right hind foot of *Spilogale putorius*.
B. Right fore foot of the same.
C. Right hind foot of *Mephitis mephitica*.
D. Right fore foot of the same.

× $\frac{1}{3}$.

Judging from dried skins and from Hodgson's unpublished drawings referred to in my paper quoted above, the feet of *Arctonyx* seem to resemble those of *Meles* in all essential particulars. The soles of the feet are quite naked. The large naked area above the plantar pad of the hind foot has two elongated thickenings representing metatarsal pads; the plantar pad of the hind foot is about as wide as long and markedly three-lobed (Hodgson probably accidentally omitted the hallucal element) and narrower than the foot; the digital pads of both feet are oval and well defined. In the fore foot the plantar pad is markedly four-lobed and wider than long, and separated from it by a considerable space are the two rather large carpal pads, which are together about as wide as the plantar pad. The pads are coarsely granular and tessellated.

The fore foot of *Mellivora* resembles that of *Taxidea* rather than that of *Meles* in the large size of the digital pads and the extension of the webbing along their edges, but the plantar pad is as wide as in *Meles*, and the pollex is shorter than in either genus. The carpal pads also are much larger than in either, the outer moiety being a large subspherical mass at least as long and half as wide as the plantar pad, while the much smaller, smooth pollical portion is also larger than in *Meles*, and the two are separated from the plantar pad by a narrower strip of integument, which has no hairs upon it. The hind foot is like that of *Meles*, except that the digital pads are larger and more fully webbed, the plantar and metatarsal pads are larger, and the rest of the metatarsal area covered with naked wrinkled skin.

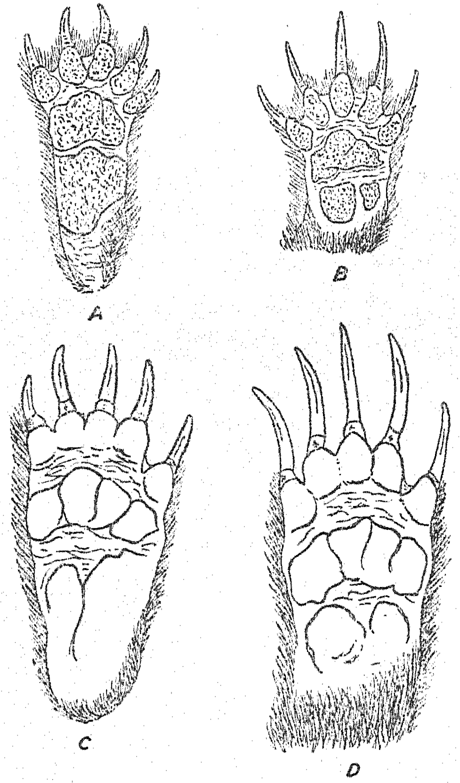
In *Spilogale*, *Mephitis*, and *Conepatus* the pads are granular and the lower surface of the feet is naked, at least as far back as the posterior border of the carpal and metatarsal pads, which are well developed. Moreover in all the examples of *Mephitis* and of *Conepatus* examined the heel from the metatarsal pad upwards is covered with naked wrinkled skin. *Spilogale* seems to have the feet less specialised for digging than the other genera, in the sense that the plantar pads are more distinctly broken up into four lobes and the carpal and metatarsal pads more reduced, the latter being, at all events in some cases, marked by a distinct longitudinal groove defining the two elements; and the third and fourth digits of the hind foot, although closer to each other than to the second and fifth respectively, have the digital pads unfused. (Text-fig. 36, A, B.)

In the several unlocalised examples of *Mephitis* examined there is naturally some variation in the size and shape of the pads, the two carpals being sometimes large and in contact, sometimes smaller and separated; but in all cases the pads are relatively larger than in *Spilogale* and less subdivided, and the digits are shorter and more fully webbed, the pads of the third and fourth of the hind foot being fused in the middle line. (Text-fig. 36, C, D.)

A further stage of specialisation is seen in *Conepatus proteus*, where the plantar, carpal, and metatarsal pads are as well developed as in any example of *Mephitis*; but the digital pads are larger and are united by webbing almost up to their proximal ends. (Text-fig. 37, A, B.)

The most highly specialised type of fossorial foot is perhaps found in *Mydaus*. The pads of the second, third, fourth, and fifth digits are fused together, except quite at their distal ends, as completely as the pads of the third and fourth digits of the hind foot are sometimes fused in *Meles*. The pads of the pollex and hallux, however, are independently movable, although attached by shallow webbing to the pad of the second digit. The soles are quite naked. The plantar pads are as wide as the feet, much wider than long, lightly arcuate, and four-lobed, the pollical and hallucal elements being large. There are two well-developed, slightly separated carpal pads, the inner being much the smaller of the two. Conjointly they are almost as wide as

Text-figure 37.



A. Right hind foot of *Conepatus proteus*.
B. Right fore foot of the same.
C. Right hind foot of *Mydaus meliceps*.
D. Right fore foot of the same.

$\times \frac{1}{3}$.

the plantar pad, from which they are separated by a short space, and there is an area of naked skin above them. In the hind foot the metatarsal area is naked to the heel and is provided with two long pads as wide as the foot, the inner being the wider of the two. (Text-fig. 37, C, D.)

The Carpal Vibrissæ.—The occurrence of these tactile hairs in many different orders of Mammals suggests that they are a primitive mammalian character. I have not mentioned them under the separate generic headings because they are present in most of the forms discussed. They are especially well developed in the active predaceous forms like *Mustela*, *Martes*, *Tayra*, *Grison*, and the Lutrinæ. In the fossorial forms they appear to be of less importance, judging from the frequent difficulty there is in distinguishing them amongst the long hairs of the leg. They are present, however, in *Lyncodon* and in *Ictonyx*. In the latter they are not always to be detected with certainty, and the tuft may be reduced to one bristle. But the sense of touch locates their position by the perception of a small wart-like swelling on the skin, where, as pointed out by Beddard, the nerve supplying the vibrissæ ends. This swelling is present in such highly specialised diggers as *Mellivora* and *Taxidea*, although I failed to differentiate the vibrissæ themselves. In *Meles*, *Mephitis*, and *Conepatus* I could find neither swelling nor vibrissæ.

The Anus and External Genitalia.

So far as is known, the normal pair of anal glands is present in all genera of the family, but they vary greatly in development. In many cases, *i. e.* in *Martes*, *Gulo*, *Tayra*, *Lutra*, *Taxidea**, *Meles*, the glands are not enlarged and the secretion is not particularly offensive in scent to Man, and is not apparently used by the animal itself for defensive purposes. But in other genera, like *Mellivora*, *Grison*, *Ictonyx*, *Mephitis*, *Conepatus*, the glands are enlarged, the secretion is copious, and is ejected at an enemy in case of attack or when two individuals of the same species fight together. And these genera are unusually coloured, being either grey above and black below or striped with white along the dorsal area†. *Putorius* also is accredited with the same habit, although the scent of the secretion is not so pungent and lasting as in the other genera mentioned. Nor is the coloration so striking; but the underfur is creamy white when the coat is lifted and this pallid hue often pervades nearly the whole body‡.

---

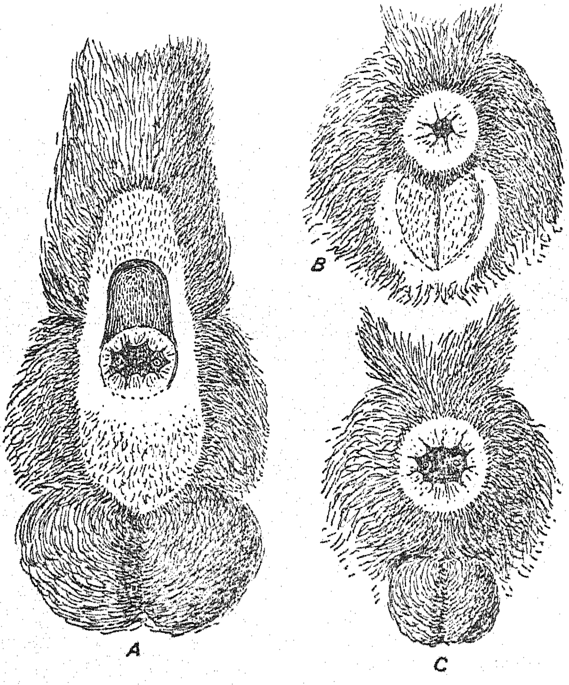
* At least in the single female example I examined.

† See my paper, "The Warning Characters of Musteline Carnivora" (Proc. Zool. Soc. 1908, p. 955). In this paper I threw out the suggestion that the similarity in colour between *Tayra* and the Canine genus *Speothos* might be an instance of mimicry, on the supposition that the secretion of the anal glands in *Tayra* might turn out to be offensive as it is in *Grison*. Since subsequent observation has shown this not the case, the suggestion must be withdrawn. It does not seem likely that *Speothos* is the offensive model mimicked by *Tayra*.

‡ See my paper on the warning coloration of *P. nigripes* (Proc. Zool. Soc. 1911, pp. 559-560).

The anus itself is typically exposed as a button-shaped convex disc, everywhere surrounded by hair as in *Martes*, *Mustela*, *Gulo*, *Lutra*, *Ictonyx*, and others; but in some cases, as in *Mellivora*, it is sunk in a circular thickening of corrugated integument, whereas in *Meles* there is a more definite thinner-walled pouch round it. In *Tayra*, again, there is above the anus a shallow depressed area, bounded on each side and posteriorly towards the root of the tail by a low ridge of skin. Possibly some modification similar to this was the origin of the deep subcaudal glandular pouch present in *Meles* and, according to accounts, in *Arctonyx*. (Text-fig. 38, A–C.)

Text-figure 38.



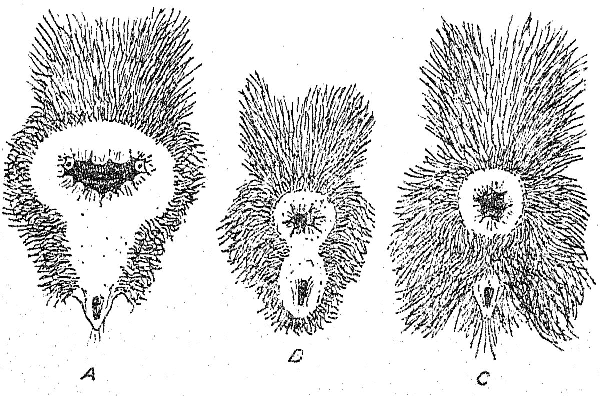
A. Anal region of *Tayra barbara* ♂, showing the naked skin around the anus and the depression above it.
B. The same of *Melogale personata* ♂, showing the scrotum close beneath the anus.
C. The same of *Grisonella* sp. from Cordova, Argentine.

× ½.

The perineal region between the anus and vulva or scrotum is thickly overgrown with hair in *Gulo*, *Martes*, *Mustela*, *Ictonyx*, and *Lutra*. It is similarly hairy in a male *Grisonella*, but in a female of the same species it is naked or scantily hairy. It is also scantily hairy in *Mellivora*, *Tayra*, *Taxidea*, *Meles*, *Mephitis*, and *Conepatus*.

In all cases examined the vulva is a fusiform excrescence with a vertical slit-like orifice, bounded on each side by two labia enclosing the clitoris and the urinary and genital orifices. (Text-fig. 39, A–C.)

Text-figure 39.



A. Anus and vulva of *Conepatus proteus*.
B. The same of *Grisonella* sp. from Cordova, Argentine.
C. The same of *Plesiogale nudipes*.

The penis is very variable in shape, in accordance with the shape of the *baculum*; but the prepuce is always situated well in advance of the scrotum, as in the Canidæ, Procyonidæ, and Ursidæ.

The Classification of the Mustelidæ.

In the classification which follows I have adopted the method employed by Gray of combining analytical headings, which give prominence to particular characters, with the definitions ordinarily found in the text-books, where the characters are set forth as if of equal value. For the interpretation of the table it is necessary to remember that contrasted headings are marked by the same letter—e. g., *a–a'*, *b–b'*, and so on. I have adopted all the sub-families originally proposed and defined by Gray and Gill, and consistency in treatment has compelled the addition of several new groups of that rank. It is not claimed that they are all of equal value. The Guloninæ, for instance, have been admitted rather as a concession to the opinion of a distinguished contemporary than as a mark of my conviction that the characters deserve the rank assigned to them. Systematists of the old school will probably criticise the classification on the grounds that most of the subfamilies are monotypical. That objection is, however, in my opinion, illogically hollow. Differentiating characters and degrees of affinity are in danger of being completely lost sight of, if structural variations are disregarded because of their restriction to an isolated genus represented by two or three, or even a single species. And I can see no logical halting-place between some such amplification of Gill's classification as that here proposed and the classification of Turner (Proc. Zool. Soc. 1848, p. 86), who admitted no names for subordinate sections in the group. Either method of dealing with the numerous genera is preferable to the superficial and dissatisfying system proposed by Flower, to which recent authors have adhered.

a. Hind feet larger than fore feet*; head, fur, tail, and limbs modified in the normal mammalian fashion for aquatic life; kidneys lobulate.

Subfamily LUTRINÆ Gray & Gill.

Skull shaped very much as in the typical Mustelinæ; cavity of bulla, where known, as in Martinæ, but with roof depressed upon auditory annulus and not extending to paroccipital process; palatine foramina maxillary. Basicranial and basifacial axes approximately in one plane. Teeth powerful, upper carnassial with talon large, nearly as long as blade; molar wider than long, but about as large as carnassial; lower carnassial with long wide heel and large metaconid. Hind feet with normally proportioned digits, the second and fifth much shorter than third and fourth. Tail long.

Genera *Lutra*, *Hydrictis*, *Lutrogale*, *Amblonyx*, *Aonyx*, *Paraonyx*, and possibly others.

In my paper on "The External Characters of some Species of Otters" (Proc. Zool. Soc. 1921, pp. 535–546), reasons were given for regarding the Otters as modified descendants of the Musteline-Martine stock of the Mustelidæ rather than of the Meline stock as suggested by Miller.

Subfamily LATAXINÆ, nom. nov.
(=*Enhydrinæ* Gray & Gill.)

Differing from the Lutrinæ in having the hind feet very large and paddle-like, with digits subequal, but the fifth slightly longer than the third or fourth; the tail short, the basicranial axis depressed at an angle upon basifacial axis; the angular of the mandible remote from the condyle; the teeth with rounded cusps, and the median lower incisor suppressed.

---

* Flower's frequently copied statement that the feet in the Lutrinæ are "short and rounded" is unintelligible. The feet of the Melinæ, on the contrary, he described as "elongated."

Genus *Latax*.

No one can doubt that *Latax* is a Lutrine profoundly modified in adaptation to marine life. The change in its method of feeding, from the capture of swift-swimming fish to the picking up and crushing of sessile molluscs or slow-moving crustaceans, has modified the teeth and skull in the way indicated; and the increase in size and alteration in structure of the hind feet, accompanied by loss of length in the tail, suggests the need for skilful turning amongst submerged rocks, rather than for swift progression through the water and comparative activity upon the land.

a'. Hind feet usually smaller, never larger than fore feet; no structural modifications subservient to aquatic life; kidneys not lobulate.

b. Cavity of bulla completely divided into two subequal chambers by oblique partition passing from the stylomastoid foramen forwards and inwards to the carotid foramen.

HELICTIDINÆ Gray & Gill.

Bulla not communicating with periotic hollow, its roof close to auditory annulus. Upper carnassial with large bicuspid talon; molar wider than long, smaller than carnassial; lower carnassial with moderate heel and large metaconid. Rhinarium very deep below nostrils, lateral slit of nostrils long and complete; no philtrum or groove on upper lip. Ear with well-developed bursa. Feet fossorial, naked below, but narrow, with webbing only extending to proximal end of digital pads, which are widely separable; all the pads coarsely striate; two long metatarsal pads. No anal pouches.

Genera *Helictis* and *Melogale*.

Although *Helictis* has been allowed by almost universal consent to retain a place in the Melinæ, where it was placed by Flower, recent examination has justified its separation from that subfamily, as I suggested last year, and its assignment to a special subfamily as proposed by Gray and Gill. The auditory bulla is quite peculiar, and the teeth are neither Meline nor Musteline; the rhinarium may be described as Meline and the ear as Musteline; the feet, although fossorial in the matter of the claws, are not so specialised for digging as those of *Meles*; the tail, moreover, is long and there is no trace of the subcaudal pouch found in that genus. Apart from the auditory bulla *Helictis* is a less specialised form than *Meles*, and is a type intermediate between the "fossorial" and "non-fossorial" members of the Mustelidæ. Its trivial name Ferret-Badger is not inappropriate.

b'. Cavity of bulla, when divided, separated into an anterior larger and a posterior smaller chamber by a transverse partition running from the stylomastoid to the foramen lacerum posticum.

c. Walls of bulla everywhere thick and permeated with air-cells continuous with those of the mastoid, the cells of which may communicate with the cavity of the bulla.

Subfamily MUSTELINÆ, s. s.

Skull with long cranial and short facial portions. Teeth sectorial, talon of upper carnassial small, anterior; molar much wider than long; lower carnassial with cuspidate heel, metaconid retained or absent; *pm.* 1 lost above and below. Tympanic annulus in contact with roof of bulla. Palatine foramina maxillary. Rhinarium small. Bursa of ear marginal, large or moderately so. Feet cursorial, usually hairy below, no metatarsal pads; other pads moderate or small, coarsely striate, claws short and curved; digits webbed to proximal end of pads, the 2nd, 3rd, and 4th widely separable. Baculum with a narrow, long, deep groove in its distal third beneath, ending in a median rounded apex.

Genera *Mustela*, *Gale*, *Plesiogale*, *Putorius* (with such subgenera of one or the other as *Lutreola* and *Kolonokus*), *Vormela*.

The restriction of the term Mustelinæ to the Stoats, Weasels, and Polecats is justified by the number of characters by which they differ from other members of the Mustelidæ. The group contains a larger number of species than any other subfamily, and, apart from the Lutrinæ, is more widely distributed. When the tropical forms are better known, other genera may be added; but perhaps characters negativing some statements in the description of the subfamily may come to light.

c'. Walls of bulla thin, its cavity either closed behind or opening into a spacious periotic hollow.

d. Cavity of bulla closed behind.

e. Teeth sectorial, approximately as in Mustelinæ, the upper carnassial being longer than wide, with the talon anterior and narrow-necked, and the molar wider than long, etc., and the line of the upper incisors nearly straight. Feet scansorial and cursorial, with short sharp claws.

Subfamily MARTINÆ, s. s.

Two carpal pads separated by hairy space from narrow plantar pad, digital webs hairy below; no metatarsal pads. A well-developed marginal bursa on ear. No trace of pouch above anus. *Pm.* 1 retained above and below. Baculum with two or four branches.

Genera *Martes* and *Charronia*.

Although usually associated with the Stoats, Weasels, and

Polecats, which they generally resemble in the structure of the feet and teeth, the Martens differ from them principally in the structure of the auditory bullæ, but also in their longer jaws, less sectorial teeth, the retention of *pm.* 1, and the position of the posterior palatine foramina on the suture.

Subfamily GULONINÆ Gray & Miller.

Chiefly distinguishable from the Martinæ by having the preorbital foramen in front of the orbit, the bullæ small, the auditory tube long, the occipital region short, the mastoid large, the upper anterior premolars separated from the lower, and the metaconid of the lower carnassial suppressed.

Genus *Gulo*.

Subfamily TAYRINÆ, nov.

Distinguishable from the Martinæ and Guloninæ by having the two carpal pads fused into a large mass as large and as wide as the large plantar pad and in contact with it, by the presence of a large metatarsal pad and naked interdigital webs and a very shallow bursa remote from the posterior edge of the ear, by the loss of *pm.* 1 above and below, the presence of a shallow subcaudal pouch, and an apically unbranched baculum.

Genus *Tayra* (=*Galera*).

The Tayra was for quite unintelligible reasons formerly regarded as congeneric with the Grison, the two being quoted as *Galictis*. They are at least as different as the Polecat is from the Marten.

e'. Teeth not of the sectorial type, the upper carnassial about as wide as long, with the talon median and arising by a long base from the blade; the molar about three times the size of the carnassial, as long as wide; lower carnassial with a long wide heel, and the metaconid as large as the other cusps; the upper incisive line curved. Feet fossorial, with long powerful claws.

Subfamily MELINÆ, s. s.

Two carpal pads separated by a naked or hairy space from the wide plantar pad; interdigital webs naked below, narrow between the digital pads; third and fourth digits of hind foot in contact; a well-developed, partially divided metatarsal pad. No trace of bursa on ear. Rhinarium very deep beneath lateral slits of nostrils. A deep subcaudal glandular pouch.

Genera *Meles* and *Arctonyx*.

I have seen no fresh specimen of *Arctonyx*, but the external form is exceedingly Badger-like. The teeth, too, are very like those of *Meles*. The cranial differences between them are well known. In the extension of the mastoid below the auditory orifice the two genera appear to be peculiar in the family, although this character is foreshadowed in *Gulo*.

d'. Cavity of bulla opening into a large or very large hollow space in the mastoid portion of the periotic.

f. Palate produced posteriorly, so that the mesopterygoid fossa is far behind the molar teeth; baculum, where known, a stout bone.

g. Rhinarium a subcircular flattish disc, continued to the edge of the upper lip by a narrow long philtrum resembling it in texture; nostrils anterior, above middle of rhinarium; the lateral slits almost obliterated. Feet fossorial, with pads of 2nd, 3rd, 4th, and 5th digits united nearly to their apices.

Subfamily Mydainæ Gray.

Skull with muzzle and dentition much as in the Melinæ, but with frontal postorbital processes absent, zygomata and mandible slender, and mastoid not produced below auditory orifice. Cavity of bulla ceasing just behind petrous portion of periotic, and opening laterally into hollow of mastoid portion of periotic by a single orifice as in the Mephitinæ. Pinna of ear reduced to a simple rim. No subcaudal pouch.

Genus *Mydaus*.

I have seen no fresh specimen of this genus, and the structure of the baculum, if developed, is apparently unknown. The Teledu has well-marked peculiarities, especially in the structure of the rhinarium and feet. The rhinarium is unique; and the only genus which shows an approach to the fusion of the digital pads is *Conepatus*. The latter also has the pinna of the ear greatly reduced with the orifice exposed, and the bulla of *Mydaus* seems to resemble tolerably closely that of the Mephitinæ; but in other respects, particularly in the long jaws, the curved upper incisive line, the long posterior palate, the backward position of palatine foramina, the genus more nearly approaches the Melinæ. If Ferret-Badger is a good name for *Helictis*, perhaps Skunk-Badger would be a suitable appellation for *Mydaus*.

g'. Rhinarium normal, nostrils much nearer its lower than its upper edge, the lateral slits long; no trace of philtrum and no groove on upper lip. Pads of 2nd, 3rd, 4th, and 5th digits free.

h. Tympanic annulus projecting as a free ridge into bulla, not confluent with its roof, the posterior rafter arched high above petrous, leaving a large space between the chambers, of which the posterior is not multiloculate; bullæ encroaching on glenoid in front.

i. Teeth sectorial, in a general way like those of Martinæ; occipital crest inclined backwards and inwards from mastoid, not semicircular from back view.

Subfamily Mellivorinæ Gray & Gill.

Periotic hollow, comparatively small, not extended to tip of mastoid, which, like the paroccipital, stands prominently away from bulla, the latter rounded in front and remote from hamular; palatine foramina on suture. Lower carnassial without metaconid; last lower molar lost; upper molar with wide cingulum. Feet very broad, digits closely tied, with large carpal and metatarsal pads in contact with wide plantar pads. Pinna of ear reduced to an integumental thickening. A glandular pouch round anus.

Genus *Mellivora*.

Subfamily ICTONYCHINÆ.
(=*Zorillinæ* Gray & Gill.)

Periotic hollow larger, extending to tip of mastoid, which, like the paroccipital, is close to the bulla; the latter pointed in front and fused with hamular; palatine foramina on maxilla. Lower carnassial with high acute metaconid; last lower molar retained; upper molar without wide cingulum. Feet narrow, but claws long, the digits widely separable; pads small, carpals separated from plantar pad; metatarsal absent. Ears with large pinna. Circumanal integument unmodified.

Genera *Ictonyx* (*Zorilla*) and *Pœcilictis*. (? *Pœcilogale.*)

i'. Teeth not sectorial; upper carnassial enormous, with very large bicuspid talon; molar a little smaller than carnassial, triangular, its inner and anterior borders subequal as in Melinæ; lower carnassial with large cuspidate heel and large metaconid; occipital crest rising nearly vertically from mastoid, and nearly semicircular from posterior aspect.

Subfamily TAXIDIINÆ Pocock.

Feet broad and fossorial with long claws as in Mellivorinæ, but plantar pads narrower, a single small carpal pad remote from plantar pad, and no metatarsal pad. No glandular pouch associated with anus. Ear with pinna well developed.

Genus *Taxidea*.

h'. Tympanic annulus confluent at its summit with roof of bulla; posterior rafter-like partition of the bulla close down upon the petrous, leaving a narrow passage between the two chambers, the posterior of which is markedly multilocular; bullæ remote from glenoid in front.

Subfamily GRISONINÆ, nov.

Teeth as in Mustelinæ, but talon of upper carnassial much larger, occupying nearly half the inner surface of the tooth; palatine foramina maxillary. Feet not fossorial, almost as in Tayrinæ, but with carpal pads farther from plantar pad. Pinna of ear well developed with bursa present, but small and in front of posterior margin. No subcaudal pouch.

Genera *Grison*, *Grisonella*.

Subfamily LYNCODONTINÆ, nov.

Differing from the Grisoninæ in cranial and more particularly in external characters. Bullæ inflated, not flattened externally towards auditory orifice, with anterior edge obliquely transverse, not emarginate; mesopterygoid fossa longer; *pm.* 2 lost above and below. Feet with long fossorial claws, but unique in the family; digits only webbed for a short distance beyond plantar pads; hairy laterally, mesially naked below, like the reduced webs. Carpal pads reduced to the external moiety which is in contact with the plantar pad, the rest of the carpal area covered with hair, which encroaches over the middle of the plantar pad; no trace of metatarsal pads; plantar pad of hind foot reduced like that of fore foot. Upper lip completely grooved. Ear greatly reduced, no trace of bursa or of valvular supratragus.

Genus *Lyncodon*.

I have seen no fresh examples of this small Patagonian genus, my observations having been made upon dried skins and skulls in the Natural History Museum. The coloration is very like that of *Grison*, with which *Lyncodon* was affiliated by Matschie, and I suggested that the likeness might be a case of Müllerian or genuine mimicry (Proc. Zool. Soc. 1908, p. 953). It cannot be claimed that the genus is closely related to *Grison*. Even the evidence that it is a very aberrant form of the *Grison*-group is not convincing, despite the resemblance between the two in the internal structure of the bulla suggested by my unavoidably imperfect examination of this portion of the skull in *Lyncodon*. The feet differ from those of *Grison* at least as profoundly as the feet of *Mustela* or *Martes* differ from those of *Meles* or *Mellivora*.

f′. Palate not produced posteriorly, the mesopterygoid fossa reaching almost up to the line of the upper molar teeth. Baculum unossified or ossified as an exceedingly slender undifferentiated rod.

Subfamily MEPHITINÆ Gray & Gill.

Cavity of bulla simple, ceasing close behind petrous, communicating with large periotic hollow by means of a small circumscribed orifice set forwards in a line with the outer end of the petrous and in front of the stylomastoid foramen, which is set far in and narrowly separated from the foramen lacerum posticum. Bulla not nearly extending to paroccipital, but encroaching on glenoid in front. Muzzle massive, but zygomata and postorbital processes weak. Teeth resembling those of the Melinæ and Mydainæ, but the upper incisive row nearly straight, the upper molar not twice the size of the carnassial and wider than long; *pm.* 1 lost above and below; palatine foramina maxillary. Feet fossorial, with soles naked, two carpal pads, and metatarsal pad; pads of 3rd and 4th digits of hind foot basally united. Ear with orifice not concealed behind tragal ridge. No pouches associated with anus.

Genera *Spilogale*, *Mephitis*, *Conepatus*.

Although the Skunks constitute a well-developed subfamily, they seem to be linked in a measure with the Melinæ through *Mydaus*. The three genera show considerable range in structure, *Spilogale* being the least, and *Conepatus* the most, specialised form, the former standing nearest to the more typical members of the Mustelidæ, such as *Ictonyx*, and *Conepatus*, in its feet, ears, and rhinarium, foreshadowing the peculiarities of *Mydaus*.

42. *Megalohyrax* Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt.

By H. Matsumoto *.

[Received October 18, 1921: Read November 22, 1921.]

(Text-figures 1–6.)

In the course of my re-study of the fossil Hyracoidea of the Fayûm, Egypt, based upon the material belonging to the American Museum and the British Museum, I found that Schlosser's identification of Andrews's genus *Megalohyrax* is incorrect, the type-specimen of the genotype *Meg. eocænus* Andrews belonging not to Schlosser's "*Megalohyrax*," but to his "*Mixohyrax*." Consequently, his "*Mixohyrax*" should be called *Megalohyrax*, while his "*Megalohyrax*" wants a new generic name. I propose to call it *Titanohyrax*, g. n.

I have the pleasure to express here my hearty thanks to Dr. Arthur Smith Woodward and Dr. Charles W. Andrews, by whom I was permitted to examine the material belonging to the British Museum.

Genus Megalohyrax Andrews.

Megalohyrax Andrews, Geol. Mag., Decade iv. vol. x. 1903, p. 341; Andrews, Brit. Mus. Cat. Tert. Vert. Fayûm, Egypt, 1906, p. 92.

Mixohyrax Schlosser, Zool. Anz., Bd. xxxv. 1910, p. 502; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, pp. 98 & 115.

This genus is to be re-diagnosed as follows:—

Long-skulled and long-snouted. Premaxillæ long, but not especially elongated supero-posteriorly. Nasals long, with acutely-pointed anterior ends, which lie nearly as anteriorly as the anterior ends of premaxillæ and a certain, but not very great, distance in front of the anterior ends of naso-premaxillary sutures. External nares not retired at all. Upper surface of skull very rough, with irregular pits and grooves with intervening ridges. Mandibular ramus shallow, with a large fenestra-like opening on the inner surface. Dental formula: $\frac{3.1.4.3}{3.1.4.3}$; I^1 and I_2 enlarged and tusk-like. Cheek-teeth bunoselenodont, brachyodont. Upper P^{1-2}, and usually also P^3, three-cusped; P^4—M^3, and sometimes also P^3, four-cusped. Paraconal and metaconal folds very weak, and especially so in the more posterior premolars and in the molars. Mesostylar fold absent in P^{1-4}. Parastylar fold of P^{1-3} very feeble; that of P^4 rather strong; both parastylar and mesostylar folds of M^{1-3} especially strong, rounded, and stout. Ridges of lower P_2—M_3 W-shaped. Metaconid simple, without differentiated metastylid. Posterior talon of M_3 very large.

---

* Communicated by Dr. C. W. Andrews, F.R.S., F.Z.S.

Genotype: *Megalohyrax eocænus* Andrews, 1903; non Schlosser, 1911.

This genus includes *Megalohyrax minor* Andrews, 1904; *Mixohyrax niloticus* Schlosser, 1910; *Mix. suillus* Schlosser, 1910; and *Megalohyrax pygmæus*, sp. n., besides the genotype.

Synopsis of Species of Megalohyrax.

(1) Extremely large species; length of upper P^{1-4} and of M^{1-3} respectively 75 mm. and 86 mm. (Andrews's type: M. 8502) .... *eocænus*.

(2) Large species; length of upper P^{1-4} and of M^{1-3} respectively 63 (Andrews's type: C. 8818)—64 (Am. Mus. 13332) mm. and 74 (Andrews's type)—78 (Am. Mus. 13332) mm.; that of lower P_{1-4} and of M_{1-3}, ca. 69 (Am. Mus. 13345)—70 (Schlosser) mm. and ca. 78 (Am. Mus. 13338)—85 (Schlosser; Am. Mus. 13345) mm. respectively.. *minor*.

(3) Rather large species; length of upper P^{1-4} and of M^{1-3} respectively ca. 54 mm. and ca. 62 mm. (Schlosser's fig.); that of lower P_{1-4} and of M_{1-3}, 55 (Schlosser)—57 (Schlosser; Am. Mus. 13334) mm. and 68 (Schlosser)—75 (Am. Mus. 13334) mm. respectively .... *niloticus*.

(4) Small species; length of lower P_{1-4} 46 mm. (Schlosser); that of lower M_{1-2} 32 mm. (Schlosser), whereas the same measurement in the immediately preceding and the next species is 42 mm. and 24–25 mm. respectively . *suillus*.

(5) Very small species; length of upper P^{1-4} and of M^{1-3} respectively 35·5–36 mm. and 37 mm. (type-specimen: Am. Mus. 14454); that of lower P_{1-4} and of M_{1-3}, 31·5 (M. 9480)—33 (type-specimen) mm. and ca. 38 (Am. Mus. 14463)—40 (type-specimen) mm. respectively . *pygmæus*.

(1) MEGALOHYRAX EOCÆNUS Andrews.

M. eocænus Andrews, Geol. Mag., Decade iv. vol. x. 1903, p. 340, text-fig. 1; Andrews, Brit. Mus. Cat. Tert. Vert. Fayûm, Egypt, 1906, p. 92, pl. vi. figs. 1 & 2 (*non* text-fig. 39).

M. 8502; type-specimen; fragment of right premaxilla and maxilla, bearing C—M^3 *in situ*.

Schlosser has failed to understand this type-specimen, hence also to identify this species and this genus. He had the opinion that the teeth of this specimen, as figured by Andrews, were erroneously restored. According to my actual observation of this specimen, Andrews's illustration proves to be fundamentally correct, though the measurements of the teeth of this specimen were confusingly misprinted (width as "length," and length as "width" in P^2—M^3). The more important dental characters of this specimen are:—(1) The premolars have no proper mesostyle (a distinctive character from *Titanohyrax*), though the external basal cingulum of P$^{2-3}$ (unknown in P^4) has a raised tubercle just outside the metacone. (2) The parastylar and mesostylar folds of the molars are very strong, rounded, and stout (a distinctive character from *Titanohyrax*). (3) The paraconal and metaconal folds of the molars are exceedingly feeble and insignificant (a distinctive character from *Geniohyus* and *Bunohyrax*). (4) The P$^{1-2}$ have no hypocone; P^3, a very rudimentary one; and P^4, a more or less well-developed one (in *Geniohyus* and *Bunohyrax*, all P$^{1-4}$ have no hypocone; in certain other species of *Megalohyrax*, P$^{1-3}$ have no hypocone and P^4 has one; and in *Titanohyrax*, all P$^{1-4}$ have a well-developed hypocone). (5) The posterior surface of the protocone of P^1—M^3 is not rounded, but is provided with a well-rounded ridge; the anterior inner surface of the hypocone of M$^{1-3}$ is not rounded, but is provided with a well-developed metaloph, which is as strong as or even stronger than the ridge on the posterior surface of the same cone (distinctive characters from *Titanohyrax*). (6) The surface of enamel of the teeth is not smooth, but very rough (a distinctive character from *Titanohyrax*). These characters indicate that *Megalohyrax* typified by this specimen does not correspond to Schlosser's "*Megalohyrax*" (=*Titanohyrax*) at all, but to his "*Mixohyrax*" (=*Megalohyrax*).

As Andrews's measurements of the teeth of this specimen were confusingly misprinted, I here give the measurements taken by me (in mm.):—

	Length.	*Width.*
C	18	11·5
P^1	17	18
P^2	17	21·5
P^3	18·5	21·5
P^4	19	—
M^1	24	—
M^2	28·5	—
M^3	34	37

Length of P^{1-4} 75
Length of M^{1-3} 86

(2) MEGALOHYRAX MINOR Andrews.

M. minor Andrews, Geol. Mag., Decade v. vol. i. 1904, p. 213; Andrews, Brit. Mus. Cat. Tert. Vert. Fayûm, Egypt, 1906, p. 97 (*pars*), pl. vii. fig. 1 (*non* figs. 2 & 3).

Mixohyrax andrewsi Schlosser, Zool. Anz., Bd. xxxv. 1910, p. 503; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 115, pl. x. (ii.) figs. 9–11.

C. 8818; type-specimen; fragment of left maxilla, bearing P^1—M^1 *in situ*.

Schlosser kept the specific name "*minor*" for a certain specimen of Andrews's and adopted a new name, "*andrewsi*," for the present species, which includes this type-specimen of *M. minor*. Such a statement as Schlosser's is, of course, against the law of priority: the name "*minor*" must be kept for the present species. The length of P^{1-4} and of M^{1-3} of this type-specimen is 63 mm. and 74 mm. respectively.

M. 9478; fragment of left mandibular ramus, bearing P_4—M_3 *in situ*, which are strongly worn.

The mandibular ramus measures 52 mm. and 64 mm. in depth at the anterior side of P_4 and of M_3 respectively. The teeth measure as follows (in mm.):—

	Length.	*Width.*
P_4	18	12·5
M_1	22·5	14·5
M_2	25·5	17
M_3	38	19

Length of M_{1-3} 85

M. 9419; small fragment of left mandibular ramus, bearing M_2 *in situ*. The molar measures 26 mm. in length and 17 mm. in width.

(3) MEGALOHYRAX NILOTICUS (Schlosser).

Mixohyrax niloticus Schlosser, Zool. Anz., Bd. xxxv. 1910, p. 503; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 116, pl. xi. (iii.) fig. 9, pl. xii. (iv.) figs. 3 & 6, pl. xv. (vii.) figs. 1, 4, & 8.

Mixohyrax suillus Schlosser, *loc. cit.* 1911, p. 118 (*pars*), pl. x. (ii.) fig. 6.

(4) MEGALOHYRAX SUILLUS (Schlosser).

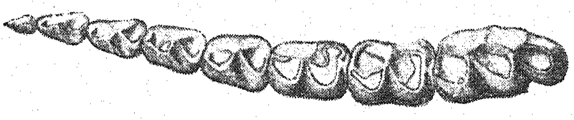
Mixohyrax suillus Schlosser, Zool. Anz., Bd. xxxv. 1910, p. 503; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 118 (*pars*; *non* pl. x. (ii.) fig. 6).

(5) MEGALOHYRAX PYGMÆUS, sp. n.

Saghatherium magnum Andrews, Geol. Mag., Decade v. vol. iv. 1907, p. 99 (*non* Andrews, 1904), text-fig. 2.

For the full description of this new species, see another paper of mine, now in preparation. The type-specimen and paratypes of this species belong to the American Museum. I will cite here only one specimen belonging to the British Museum, which is to be referred to this species.

Text-figure 1.



Megalohyrax pygmæus, sp. n., Matsumoto. Crown view of left lower C—M_3; natural size; M. 9480; referred specimen, not the type.

M. 9480; left mandibular ramus bearing C—M_3 *in situ* (text-fig. 1). The mandibular ramus is very shallow (though crushed just a little, it can by no means be restored to a ramus so deep as in *Saghatherium*) and has a large fenestra-like opening on the inner surface (distinctive characters from *Saghatherium*).

A full description of this new species is given elsewhere.

The measurements of the teeth were as follows (in mm.):—

	Length.	*Width.*
C	4·5	2·7
P_1	7	4·4
P_2	7·7	5
P_3	8	6
P_4	8·7	7·2
M_1	10·7	7·5
M_2	11·8	8·5
M_3	17·5	9·6

Length of P_{1-4} .... 31·5

Length of M_{1-3} 39

Genus TITANOHYRAX, g. n.

Megalohyrax Schlosser (*non* Andrews, 1903), Zool. Anz., Bd. xxxv. 1910, p. 502; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, pp. 97 & 104.

This genus is diagnosed as follows:—

Skull very imperfectly known (laying aside the problematical specimen C. 8801, which may possibly be referred to this genus), but judging from the shape of premaxillæ and mandible and from the dental series of both jaws, this genus might be more or less short-skulled and short-snouted. Premaxillæ exceedingly elongated supero-posteriorly; their anterior ends lying a great distance in front of the anterior ends of naso-premaxillary sutures. Judging from the shape of the premaxillæ, the external nares may be retired backwards instead of being terminal. Mandibular ramus shallow, without fenestra-like opening. Dental formula: $\frac{3.1.4.3}{3.1.4.3}$; I^1 enlarged and tusk-like; none of lower incisors tusk-like. Cheek-teeth selenodont, brachyodont, though rather high. All upper P^1—M^3 four-cusped. Paraconal and metaconal folds somewhat indistinct except in P^1. Mesostylar fold present in all P^1—M^3. Parastylar and mesostylar folds trenchant instead of being rounded. Ridges of lower P_2—M_3 W-shaped. Metastylid well differentiated from metaconid. Posterior talon of M_3 rather small.

Genotype: *Megalohyrax palæotherioides* Schlosser, 1910.

This genus includes *T. ultimus*, sp. n.; *T. schlosseri*, nom. n.; and *T. andrewsi*, sp. n., besides the genotype.

Synopsis of Species of Titanohyrax.

(1) Extremely gigantic species, being the largest of all the hyracoids hitherto known, upper and lower M 2 measuring about 40 mm. in length, whereas those of the next species measure about 30 mm. .... *ultimus.*

(2) Gigantic species; length of upper P^{1-4} and of M^{1-3} respectively 70 mm. and 84 ? mm. (Schlosser); that of lower P_{1-4} and of M_{1-3}, ca. 70 mm. and 94 mm. respectively (Schlosser). *schlosseri.*

(3) Large species; length of upper P^{1-4} and of M^{1-3} respectively ca. 73 mm. and 75 mm. (Schlosser); length of lower M_1 22 mm. (Schlosser), whereas the same of the immediately preceding and the next species measures 24·5 mm. and 20 mm. respectively; lower cheek-teeth of long and narrow type; snout rather long, the distance

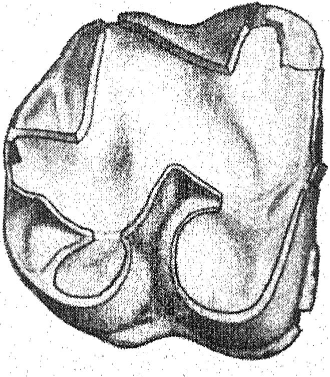
from the tip of mandibular symphysis to the posterior side of lower Dm_4 measuring ca. 114 mm. in a young individual with functional milk-molars (Schlosser's fig.) .... *palæotherioides*.

(4) Rather small species; length of lower M_{1-3} 76 mm. (type-specimen: C. 8822–3); lower cheek-teeth of short and wide type; snout very short, the distance from the tip of mandibular symphysis to the posterior side of lower P_4 measuring only 86 mm. in an old individual with much worn premolars and molars (type-specimen) .... *andrewsi*.

(1) Titanohyrax ultimus, sp. n.

M. 12057; type-specimen; isolated, right upper M^2.
M. 12058; paratype; isolated, left lower M_2.
M. 12059; paratype; isolated, left upper P^4.
M. 9479; paratype; isolated, left upper C.

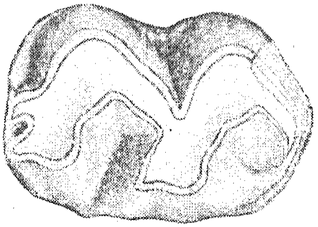
Text-figure 2.



Titanohyrax ultimus, g. & sp. n., Matsumoto. Crown view of right upper M^2; natural size; M. 12057; type-specimen.

The M^2, the type-specimen, is strongly worn (text-fig. 2). The acute mesostylar fold is a generic character; the parastylar folds are broken away in this specimen. The outer surface of both the paracone and metacone are distinctly concave, without distinct paraconal and metaconal folds, also a generic character. The inner to posterior surface of the protocone and the anterior to inner surface of the hypocone are smoothly rounded, without any ridge, also generic characters. The anterior and inner basal cingula are continuous to each other, extending from the anterior side of the protocone to the anterior half of the inner surface of the hypocone.

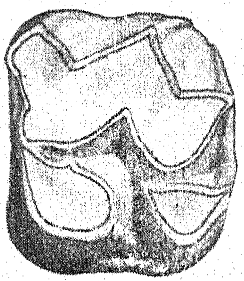
Text-figure 3.



Titanohyrax ultimus. Crown view of left lower M_2; natural size; M. 12058; paratype.

The M_2 is moderately worn (text-fig. 3). The worn area, as well as the lophids as a whole, is W-shaped. The differentiation of the metastylid from the metaconid (a generic character) is rather feeble, being feebler than that in the other smaller species of this genus. The entostylid is differentiated from the entoconid, being as well differentiated as the metastylid is from the metaconid; this differentiation is obviously more intense than that in the other smaller species. The anterior and posterior basal cingula are well developed; the latter has a distinct tubercle, just behind the posterior transverse ridge and outside the entostylid. The outer basal cingulum is feeble, being represented by a few rather insignificant crenulæ between the bases of the protoconid and hypoconid.

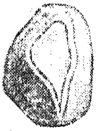
Text-figure 4.



Titanohyrax ultimus. Crown view of left upper P^{4}?; natural size; M. 12059; paratype.

The $P^{4?}$ is well worn (text-fig. 4). The parastylar and mesostylar folds are very acute. The outer surface of the paracone is distinctly concave, while that of the metacone is rather flat. The worn area of the protocone is oval, with an acute prolongation exter-anteriorly. The inner to posterior surface of the protocone is smoothly rounded, while the outer-anterior side of the hypocone has a feeble ridge. The anterior and inner basal cingula are well developed, but not continuous to each other.

Text-figure 5.



Titanohyrax ultimus. Crown view of left upper C; natural size; M. 9479; paratype.

The upper C is moderately worn (text-fig. 5). It is ovoid in palatal view. The worn area has an acute prolongation, which stretches backwards. The inner cingulum is well developed, extending from the anterior end to the posterior end of the tooth.

The teeth above described measure as follows (in mm.):—

	Length.	*Width.*
Up. C.........	16·5	12·5
$P^{4?}$	32	34·5
M^2	41	46
M_2	39	28

(2) TITANOHYRAX SCHLOSSERI, nom. n.

Megalohyrax eocænus Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 105 (*non* Andrews, 1903), pl. xi. (iii.) fig. 7.

Judging from Schlosser's description and figure, there is no doubt that his specimens of his "*Megalohyrax eocænus*" belong really to his "*Megalohyrax*," viz. *Titanohyrax*, though Andrews's *Megalohyrax eocænus* does not. So that Schlosser's specimens want a new name.

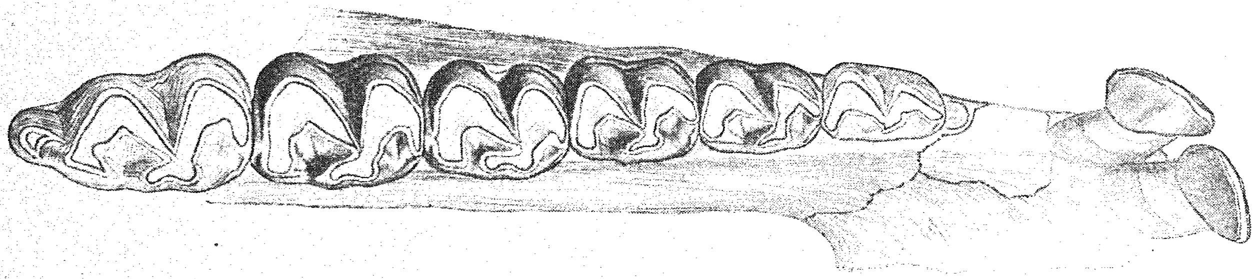
(3) TITANOHYRAX PALÆOTHERIOIDES (Schlosser).

Megalohyrax palæotherioides Schlosser, Zool. Anz., Bd. xxxv. 1910, p. 502; Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 106, pl. xi. (iii.) fig. 1, pl. xii. (iv.) fig. 1.

(4) TITANOHYRAX ANDREWSI, sp. n.

Megalohyrax minor Andrews, Brit. Mus. Cat. Tert. Vert. Fayûm, Egypt, 1906, p. 97 (*pars*; *non* Andrews, 1904), pl. vii. figs. 2 & 3 (*non* fig. 1); Schlosser, Beitr. z. Pal. u. Geol. Österreich-Ungarns u. d. Orients, Bd. xxiv. 1911, p. 105.

Text-figure 6.



Titanohyrax andrewsi, g. & sp. n., Matsumoto. Upper view of left mandibular ramus, with I_{1-2} and P_2—M_3 (P_2 and M_3 in this figure were restored after those of the right side); natural size; C. 8822–3; type-specimen.

C. 8822–3; type-specimen (text-fig. 6); large fragment of right mandibular ramus, bearing P_2—M_3 *in situ*, and large fragment of left mandibular ramus, including a greater part of symphysis, bearing $I_{1\,\&\,2}$ and P_3—M_2 *in situ*; it is almost certain that these two rami belong to one and the same mandible.

The symphysis of this mandible is quite different from that of the other genera of the Fayûm hyracoids: it is rather short and very deep, with the anterior lower side very steep; it rather resembles the mandibular symphysis of a tapir. None of the lower incisors is tusk-like. Both $I_{1\,\&\,2}$ are alike spatulate, with flat, wide, and thin crowns; their roots are clavate, with constricted proximal parts. Unfortunately, the part of the dental arch corresponding to I_3 and C is broken away in this specimen; I_3 and C must be very reduced, if they were present at all, as can be judged from the very short distance from I_2 to premolars. The mandible measures as follows (in mm.):—

Length of symphysis	50
Depth of the same	37¾
Length from tip of symphysis to posterior end of P_4	86
Depth of ramus at anterior side of P_4	42
Ditto at anterior side of M_3	53

All the cheek-teeth are moderately to strongly worn. The entostylid is not well differentiated from the entoconid. All the cheek-teeth are short and wide. The $M_{1\,\&\,2}$ have a tubercle, as a part of the posterior basal cingulum, just behind the posterior transverse ridge.

The teeth of this specimen measure as follows (in mm.):—

	Right.		*Left.*	
	Length.	Width.	Length (transverse diameter in I).	Width (antero-posterior diameter in I).
I_1	—	—	14·3	7·5
I_2	—	—	15·7	7·5
P_2	17	11·4	(14) (roots).	—
P_3	17	13·5	16·5	13·5
P_4	18	16·5–*a*.	18	15
M_1	19	16·3	20	16
M_2	23·5	19	23·5	18·5
M_3	32·5	19	—	—

Length of M_{1-3} 76

M. 9220; paratype; fragment of left mandibular ramus, bearing P_3—M_3 *in situ*: P_4, M_1, and M_3 being imperfectly represented. The mandibular ramus, as well as the teeth, is smaller than that of the foregoing specimen. It may be possible that this specimen belongs to a female, and the foregoing one to a male.

The ramus measures as follows (in mm.):—

Depth of ramus at anterior end of P_4	34
Ditto at anterior end of M_3	37
Ditto at posterior end of M_3	45
Height of ascending bar at condyle	120±
Minimum height of the same at the concavity between condyle and coronoid process	116
Minimum antero-posterior width of the same just below condyle	55

The teeth measure as follows (in mm.):—

	Length.	*Width.*
P_3	16·5	12·5
P_4	—	14
M_1	—	15·5±
M_2	21	18
M_3	30±	—

C. 8801; fragment of posterior part of skull, including occiput (? this genus and species).

It is almost certain that this skull, illustrated by Andrews in his text-fig. 39, Cat. Tert. Vert. Fayûm, Egypt, 1906, does not belong to either *Geniohyus* or *Megalohyrax*, since it differs very much from the known skulls of these genera. Naturally, there may be a possibility that it belongs to *Titanohyrax*, and even to the present species, though of course it is not certain at present.

43. Contributions to the Visceral Anatomy and Myology of the Marsupialia. By Charles F. Sonntag, M.D., F.Z.S., Anatomist to the Society.

[Received October 5, 1921: Read November 22, 1921.]

(Text-figures 70–79.)

Contents.

	Page		Page
Ventral Mesentery	851	Urinary Organs	867
Adipose Tissue	851	Ductless Glands	868
Cervical Lymphatic Glands	851	Respiratory Organs	870
Muscular System	852	Vagus and Sympathetic	873
Mouth	854	Systematic	877
Salivary Glands	857	Summary and Conclusions	880
Alimentary Canal	861	Bibliography	881
Organs of Circulation	865		

The present paper is based on the examination of several Polyprotodont and Diprotodont Marsupials * which died in the Society's Gardens; and the material comprised both fresh and preserved specimens.

I have used my paper on the Koala and Vulpine Phalanger for purposes of comparison (**15**), and I have drawn attention to the differences between the anatomy of *Perameles obesula* and that of *Cænolestes obscurus*, recently described by Osgood (**9**).

When the abdomen of *Dendrolagus ursinus* was opened an avascular peritoneal fold, representing the remains of the ventral mesentery, was seen running from the pelvic floor posteriorly to beyond the urinary bladder anteriorly. Beddard (**1**) observed a similar condition in *D. bennetti* and *Ornithorhynchus*.

Adipose Tissue:—Owen (**10**) states that the omentum of the Opossums has no fat when there are accumulations elsewhere. In *Petaurus sciureus* the omentum is heavily laden with fat, and there are deposits in other parts. The fat in the anterior part of the thorax contains the thoracic lobes of the thymus gland.

Cervical Lymphatic Glands:—The relative positions of the two groups of glands in the Marsupialia have already been described in my paper on the Koala (**15**), but the number of glands in each varies. The anterior group has only one in *Perameles obesula* and *Cænolestes obscurus*, but several are present in *Dendrolagus*

---

* Didelphyidæ: *Didelphys azaræ*, *D. marsupialis*, *D. albiventris*, *Metachirus opossum*, *Philander laniger*, *Marmosa elegans*; Dasyuridæ: *Dasyurus viverrinus*, *Sarcophilus harrisi*; Peramelidæ: *Perameles obesula*; Macropodidæ: *Macropus bennetti*, *M. giganteus*, *M. rufus*, *M. melanops*, *Dendrolagus ursinus*, *Onychogale lunata*, *Bettongia penicillata*; Phalangeridæ: *Petaurus sciureus*, *P. breviceps*, *P. breviceps papuanus*, *Pseudochirus peregrinus*, *Phalanger orientalis*, *Petaurus australis*. Duplicates of some adult forms, and a number of pouch specimens of different ages were examined.

ursinus. *Phascolarctos cinereus* has the greatest number in the posterior group, and the parathyroids may be included among them.

The only Marsupial with exoccipital processes touching the deep aspect of the platysma is *Phascolarctos cinereus*.

The Muscular System.

As considerable attention has already been paid to the muscles of the Marsupialia, the present section is limited to some points in the myology of the head and neck.

The Platysma:—The origin, insertion, and relations are similar in all Marsupials, but the characters differ considerably. In *Dendrolagus ursinus* and *Macropus rufus* it is muscular in the face, but almost aponeurotic in the neck. In *Perameles obesula*, on the other hand, it is muscular and thick in the neck, but more aponeurotic and firmer in the face; and it arises posteriorly from an equally strong and thick panniculus carnosus. In some parts these muscles are nearly two millimetres thick, and it is difficult to tell where the one ends and the other begins. The panniculus is very thick over the pectoral region. These conditions are reversed in *Cœnolestes obscurus*, in which Osgood described a thin panniculus and platysma. The platysma of *Sarcophilus harrisi* (text-fig. 70 A) is muscular throughout, and its fibres cross at the anterior extremity of the interramal space. Beneath it there lies a stratum of more or less transverse fibres which fuse with it at the sides of the neck. Although the latter cannot be traced to an attachment in the face, they may correspond to the sterno-facialis of some of the higher Mammalia, e. g. *Octodon* and the Carnivora. The condition present here may indicate that the sterno-facialis arises from the platysma by splitting.

The Sterno-mastoid and Cleido-mastoid:—Carlsson (**2**) showed that they are fused throughout the greater part of the neck in *Dendrolagus dorianus* and *Petrogale penicillata*, but not in *Trichosurus vulpecula*; and they are similarly fused in *Dendrolagus ursinus*. In a pouch specimen of *Macropus giganteus* they fuse much farther forwards; but the muscles of *Petaurus sciureus* run parallel to one another, and are only fused at their cranial insertions. Osgood (**9**) records a similar condition in *Cœnolestes obscurus*, so it differs greatly from that in *Perameles obesula*, in which the cleido-mastoid arises from the cephalo-humeral and fuses with the cranial end of the sterno-mastoid. In *Philander laniger*, *Metachirus opossum*, and *Didelphys* the sterno-mastoid, cleido-mastoid, and cleido-occipital form a group of three almost parallel muscles traversing the neck obliquely from behind forwards. In all species examined except *D. azaræ* they had separate origins from the clavicle; but in that species the cleido-occipital was implanted by tendon into the cleido-mastoid at its posterior extremity.

The posterior triangle of the neck is obliterated in *Dendrolagus ursinus* and *Petrogale xanthopus*, in which the trapezius is in contact with the sterno-mastoid. In all other Marsupials the posterior triangle is evident, and its most prominent structure is the external jugular vein. The descending cutaneous nerves emerge from between the muscles in *Dendrolagus* (text-fig. 74).

The *Omo-hyoid* is present in all Marsupials, and is strap-like or fusiform. A central tendon is present in *Macropus rufus* (**19**) and a slight one exists in *Petrogale xanthopus* (**13**). In a pouch specimen of *Macropus giganteus* (text-fig. 71 *a*) it crosses the lateral thyroid lobe which projects beyond the pretracheal muscles, and Osgood (**9**) figures it crossing the anterior lymphatic gland in *Cænolestes obscurus*.

The *Sterno-hyoids* form a uniform strip from origin to insertion in all Marsupials except a male pouch specimen of *Macropus giganteus* (text-fig. 71 *c*), in which they diverge at their hyoid attachments, and the larynx protrudes between them. They are easily separated, as a rule, from the subjacent sterno-thyroids, but that cannot be done in *Perameles obesula*. This would show that these muscles arise from a single sheet by splitting.

In my paper on the Koala and Vulpine Phalanger (**15**) I showed that the mylo-hyoid, digastric, and sterno-hyoid muscles of the former form a thin sheet playing over, but in no way connected to the hyoid bone; but I did not observe this condition in any other Marsupial; it may also be an abnormality in the animal examined by me. And in no other were there so many small muscle bundles running between the digastrics and surrounding muscles. The fusion of the digastric and mylo-hyoid supports Gegenbaur's view that these muscles were differentiated by splitting.

The *Digastric* has a small central tendon in *Macropus*, but none is present in *Dendrolagus*, *Perameles*, and *Metachirus*. In *Petrogale xanthopus* (**13**) there are small fibrous areas, but no true central tendon. The mandibular insertion is usually about half the length of the bone between the angle and the symphysis, and is usually muscular, but Osgood (**9**) gives a more extensive attachment from angle to symphysis in *Cænolestes obscurus*; and the anterior part is more aponeurotic.

The *Hyoglossus* was absent in my specimen of *Phascolarctos cinereus*, and is not described in Macalister's paper on the same animal. It is present in all other Marsupials. Its absence in the Koala is probably due to the long interval between the tongue and the hyoid bone, which has few attached muscles.

Carlsson (**2**) described the myology of *Dendrolagus dorianus* in detail, and grouped the muscles in three sets :—

1. Those resembling the muscles of the terrestrial Macropodidæ and differing from those of the Phalangeridæ.
2. Muscles resembling those of the Phalangeridæ and differing from those of the terrestrial Macropodidæ.
3. Conditions which differ from those of the terrestrial Macropodidæ and Phalangeridæ, and are secondary adaptations for an arboreal life.

My own observations on *Dendrolagus ursinus* confirm those of Carlsson.

The *stylo-hyoid ligaments* are most prominent in *Phascolarctos cinereus*.

I was unable to detect any condition foreshadowing the sterno-maxillares of the Edentata in the insectivorous Peramelidæ.

The Mouth.

The lips are fleshy in all Marsupials, and the upper one is cleft to a variable depth in the Macropodidæ, but entire in all Polyprotodonts. An incipient cleft is present in *Cœnolestes obscurus*. They are relatively thicker and always entire in the new-born animal. They bear numerous hard, rounded, or pointed tubercles in many species; in the Didelphyidæ they are absent in *Metachirus opossum*, *Philander laniger*, *Marmosa elegans*, and *Didelphys marsupialis*, but they are situated close to the angles of the mouth in *Didelphys azaræ*. In *Dasyurus viverrinus* they are situated at the level of the canine teeth. They are close to the angles of the mouth in *Dendrolagus*, *Pseudochirus*, and *Trichosurus*. The largest tubercles observed by me were in *Dendrolagus ursinus*. They are never so numerous as the papillæ in the Felidæ. In some forms the lips have callous pads.

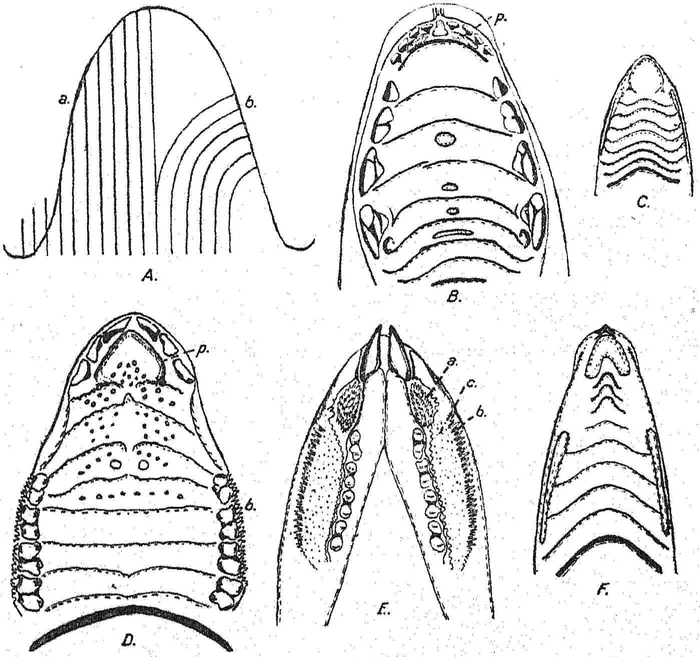
Both labial frenums are present in all genera except *Dendrolagus* and *Pseudochirus*, which have only the upper one. In the young animal it passes between the incisor teeth to be attached to the anterior end of the incisive palatal pad, but it is fixed to the gum in the adult. In a young *Æpyprymnus rufescens* it is continuous with the median crest, running back on the anterior end of the palate. The lower lip is united to the sides of the gums by comb-like crests in *Dendrolagus* and *Pseudochirus*, and these form shaggy pads in the vestibule (text-fig. 70 E, *a*).

Labial labrets are present in *Phascolomys* and *Cœnolestes*. Owen (**10**) pointed out that the labial glands are well developed in *Dasyurus*, but I did not observe orifices in *D. viverrinus*.

The mucosa lining the vestibule is smooth in all Didelphyidæ, *Sarcophilus harrisi*, *Trichosurus vulpecula*, and *Petaurus sciureus*. It is covered with innumerable closely-set, rounded papillæ of moderate size in *Dasyurus viverrinus* and *Phascolarctos cinereus*, but these are not arranged in rows like the papillæ of the Ungulata. In many Marsupials it is traversed by ridges of various kinds, which, in some cases, if not in all, are modified and fused papillæ. They are thick and entire in *Perameles obesula* and *Petaurus breviceps papuanus*, and the spaces between them probably serve as traps for insects in the former. Their free borders are nodulated in the latter. They are thin and comb-like in *Macropus*, *Æpyprymnus Pseudochirus*, and *Dendrolagus* (text-fig. 70 D, *b* & E, *b*); and their function may be to keep the spaces between the teeth clear of food particles, for they fit into them.

Cheek-pouches have been described in several species. They are large in *Chironectes* (**10**) and *Cœnolestes* (**9**), intermediate in size in *Phascolarctos*, and small in *Peragale lagotis* (**10**); but I do not think that the small fossæ of *Perameles obesula* can be dignified by the name of cheek-pouches. Forbes mentions rudimentary ones in *Phascolomys*. No Marsupial has comb-like structures on the tongue like the Ungulata.

Text-figure 70.



A. The platysma of *Sarcophilus harrisi* showing superficial (*a*) and deep (*b*) fibre B–F. The palates of *Sarcophilus harrisi* (B), *Onychogale lunata* (C), *Dendrolagus ursinus* (D), and *Macropus bennetti* (F). E. Vestibule of *Dendrolagus ursinus*; *c*. papillæ. Other letters in text.

The Hard Palate:—In many Marsupials the anterior end has an eminence, or "incisive pad," whose long axis usually coincides with that of the palate; it is at right angles to it, however, in *Sarcophilus harrisi* (text-fig. 70 B, *p*). It is smooth, papillose, or tuberculated, and varies greatly in prominence. In *Phascolarctos cinereus* and some of the Phalangeridæ it is replaced by a cluster of incisive tubercles, and its place is taken by a short, incisive ridge in *Æpyprymnus rufescens*.

The complete palatal ridges are most numerous in the Peramelidæ and *Cœnolestes obscurus*, fewest in *Trichosurus vulpecula*, and largest in *Phascolarctos cinereus*, but the commonest number is eight. They are most variable in the Polyprotodonts, and the numbers of complete and incomplete ridges are of considerable value for purposes of classification, as shown in the table of formulæ given below.

In all Marsupials the ridges on the anterior part of the hard palate are larger than those on the posterior part, and the posterior margin of the palate frequently appears as a well-marked ridge. The spaces between the ridges are occupied by papillæ, tubercles, or incomplete ridges, and the latter are present in *Didelphys*, *Perameles*, *Dasyurus*, *Sarcophilus*, and *Cœnolestes*. The incomplete ridges cross the mid line, and differ from those of many of the higher Mammalia, in which they run from a median raphé to the sides of the palate.

No Marsupial has a median raphé running the whole length of the palate.

In a very young pouch specimen of *Onychogale lunata* the lips are entire, the tongue is excavated to form a bed for the nipple, and the incisive pad and anterior palatal ridges are outlined and hardly elevated; but the posterior palatal ridges are well-marked. The conditions are such that there is a firm area of contact between the nipple and mouth. In an older pouch specimen of *Macropus bennetti* the upper lip is cleft, the incisive pad is more prominent, and the anterior palatal ridges are more developed than those of *Onychogale*; and in pouch specimens of *Macropus giganteus* and *Phalanger orientalis* of still more advanced ages the conditions resemble those of the adult—namely, large incisive pads, strong anterior ridges, and weak posterior ones.

In animals requiring a firm contact between the mouth and nipples large anterior ridges would be disadvantageous, and they are unnecessary while the diet consists entirely of milk.

The vestibule and cavum oris communicate posteriorly behind the last molar teeth, and in several Marsupials the diastemata form anterior communications.

The *Soft Palate* is frequently covered with papillæ, which are small, but visible to the naked eye. It has no uvula, and thins out posteriorly where it forms the anterior and lateral boundaries of the posterior extremity of the nasal tube; the orifice of the tube is round and small, or long and pyriform or slit-like. The larynx may be gripped by the tube, or the opening of the tube may overlap its superior aperture. In the mammary fœtus the larynx passes into the nasal tube so that the entrance of air is not impeded in suckling *.

In all Marsupials the orifices of the Eustachian tubes are within the nose. And these have been figured in my paper on the Koala and Vulpine Phalanger (**15**). They are not surrounded by a cushion.

---

* In a manuscript note Garrod states that the soft palate shuts off the glottis from the mouth in *Tamandua tetradactyla*, and suggests that this arrangement comes into use when the animal is collecting masses of termites before swallowing. No insects can possibly enter the larynx in consequence.

The characters of the palate can be conveniently expressed by means of formulæ. In the following list C denotes complete ridges, I incomplete ridges, P incisive pad, T incisive tubercles, R a median incisive ridge or raphé, and U uvula. For the area surrounded by the incisor and canine teeth the term "*incisive area*" is suggested.

POLYPROTODONTS.	
Metachirus opossum	$C_8I_0P\ \ U-$
Philander laniger ...	C_8I_1P+U-
Didelphys azaræ ...	C_9I_1P+U-
,, *marsupialis*	C_9I_1P+U-
Marmosa elegans ...	C_9I_0P-U-
Perameles obesula ...	$C_{11}I_5P+U-$
Dasyurus viverrinus	C_8I_3P+U-
Sarcophilus harrisi...	C_7I_5P+U-

DIPROTODONTS.	
Phascolarctos cinereus	C_9I_0TU-
Trichosurus vulpecula	C_6I_0P-U-
Pseudochirus peregrinus	C_8I_0P-U-
Petaurus sciureus ...	C_8I_0TU-
,, *breviceps papuanus*	C_8I_0P+U-
Cœnolestes obscurus ...	C_9I_5P+U-
Æpyprymnus rufescens	C_7I_0RU-
Dendrolagus (all species)	C_8I_0P+U-
Macropus (all species)	C_8I_0P+U-
Onychogale lunata ...	C_8I_0P+U-
Phalanger orientalis...	C_9I_0P+U-

The only Marsupial in the above list in which the palate narrows from before backwards is *Æpyprymnus rufescens*. In the Peramelids the palate is long and narrow.

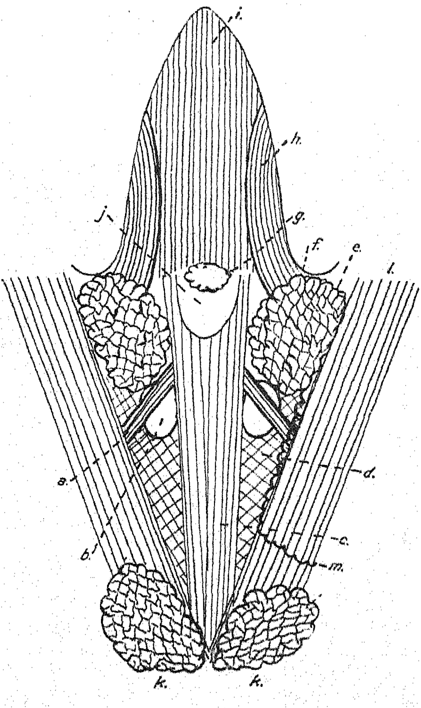
I have nothing to add to existing descriptions of the tonsils and fauces. And in no Marsupial could I detect Waldeyer's lymphatic ring in the pharynx.

The Salivary Glands (text-figs. 71–74).

The *Parotid Glands* (*m*) are small in all Polyprodonts, but vary considerably in thickness and superficial extent in the Diprotodonts. They are thick, and extend from the auricles to the clavicles in *Dendrolagus* and *Dorcopsis*, and Garrod has figured their surface markings in the latter (**4**). Their relations in the former are shown in text-fig. 74; and the ducts, which are capacious and thin-walled within the glands, become thicker and contracted where they cross the masseter muscles. They are equally thick, but only reach the middle of the neck in *Phascolarctos cinereus*. And in none of these genera do they pass mesially to the inner borders of the sterno-mastoid muscles. In other genera they are thin, and cover a variable extent of the neck. They reach the clavicles in *Petaurus*, but do not extend so far in *Macropus*, *Æpyprymnus*, and *Onychogale*.

The most extensive parotids are present in *Pseudochirus peregrinus*, in which they extend from the auricles to the clavicles, and pass inwards to cover the posterior fourth of the ventral surface of the neck. The glands are composed of numerous small portions surrounded by connective tissue, but it is not always possible to discern the ductules. They were prevented from reaching the mid line of the neck by the cervical thymic lobes in my specimen of *Trichosurus vulpecula*, but Symington (**17**) saw them cover the thymus in his. Although their extent is great they are thin.

Text-figure 71

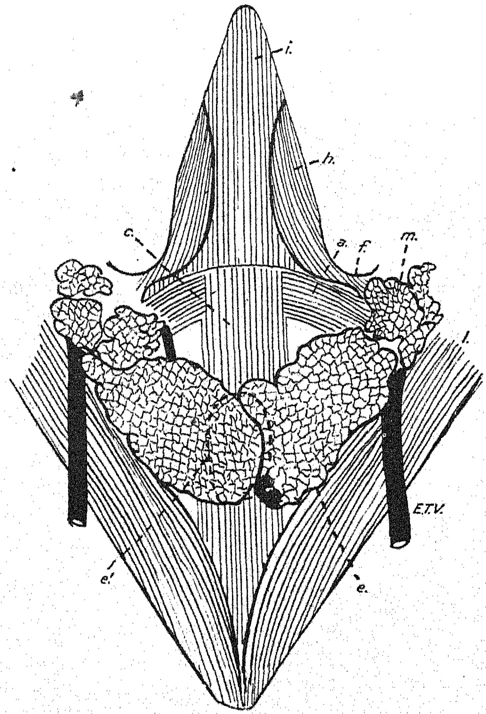


The neck of *Macropus giganteus*. *a.* omo-hyoid; *b.* thyroid gland; *c.* pretracheal muscles; *d.* fascia; *e.* submaxillary gland; *f.* mandible; *g.* small gland; *h.* digastric; *i.* mylo-hyoid; *j.* larynx; *k.* cervical thymus; *l.* sterno-mastoid; *m.* parotid gland in outline.

The *Submaxillary Glands* (*e*) are, generally speaking, large in Polyprotodonts and small in Diprotodonts, but there are exceptions in the latter. They are large, single, and oval in the Didelphyidæ and Dasyuridæ, and in some of the former they reach from the angles of the mandible to the clavicles. They are immense and lobulated in *Perameles obesula* (text-fig. 72), in which a copious viscid secretion is required to surround and entangle the insects trapped in the cheek-pouches (?) and spaces between the palatal ridges and oral vestibule; and large glands are also present in the insectivorous *Cænolestes obscurus* (9)*. In *Sarcophilus harrisi* the total mass of salivary glands is small, but the submaxillaries form the chief part.

In the Diprotodonts the submaxillary glands are single or lobulated, and the largest ones are present in the various species of *Dendrolagus*. Small isolated glands are present between the main masses in *Macropus giganteus* (text-fig. 71, *g*), but the small glands are united to the main masses in *Dendrolagus ursinus* (text-fig. 74, *g*). And in these genera I traced small sympathetic

Text-figure 72.



The neck of *Perameles obesula*. *e'*. concealed lobe of submaxillary gland; E.T.V. external jugular vein. Other letters as in text-fig. 71.

---

* In insectivorous Marsupials the glands are relatively smaller than those in the insectivorous Edentata.

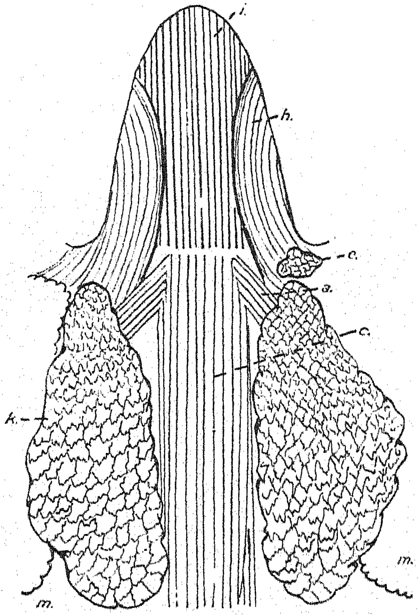
nerves into the small glands (text-fig. 78, *sgn*). The ducts do not open on frenal lamellæ as in the Primates.

One must be careful not to confuse the submaxillary glands with the cervical lobes of the thymus gland, and histological examination must be carried out in doubtful cases.

The *Sublingual Glands* of many Marsupials have already been described, and Oppel (**8**) has collected the various observations.

In *Dendrolagus ursinus* they are long, thin, and narrow, and resemble those of *D. dorianus* already described by Carlsson (**2**).

Text-figure 73.



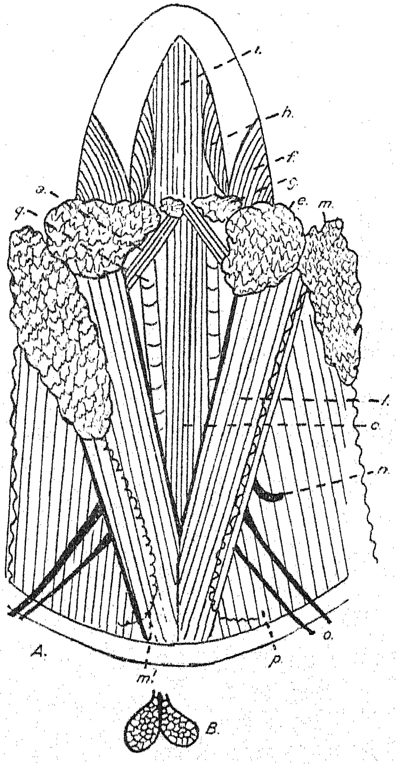
The neck of *Petaurus sciureus*. Letters as in text-fig. 71.

Osgood (**9**) described large round glands in *Cænolestes obscurus*. Those of *Perameles obesula* are oval and do not extend so far forwards. Posteriorly they are in contact with the submaxillaries. The submaxillaries are large and the sublinguals small in *P. obesula*, but the conditions are reversed relatively in *C. obscurus*.

When the total bulk of the salivary glands of each Marsupial are compared, it is seen that *Dendrolagus* has the largest mass. And they conceal large areas of the muscles in the vicinity of the hyoid bone.

I have nothing new to add to our knowledge of the arterial supply and venous drainage of the salivary glands. And I could not detect any connection between them and the anterior cervical lymphatic glands.

Text-figure 74.



The neck of *Dendrolagus ursinus* (A) and the cervical thymus B. *n*, *o*, cutaneous branches of the cervical plexus; *p*. trapezius; *q*. common carotid artery. Other letters as in text-fig. 71.

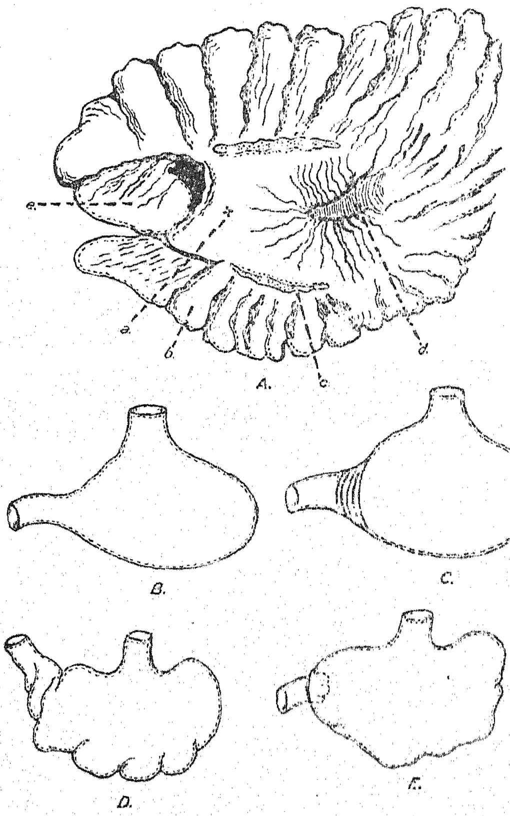
The Alimentary Canal.

The Œsophagus:—The mucosa of the abdominal part exhibits transverse rugæ in *Didelphys*, but in no other genus.

The Stomach:—The form depends on the degree of distension, but the latter is not stated in all existing accounts. Owen described a globular stomach in several species, but I found that the empty stomach is more or less triangular in a number of Polyprotodonts.

In *Perameles obesula* (text-fig. 75 B) the empty stomach is triangular with the apex formed by the œsophageal orifice. The left rounded basal angle represents the fundus, and the duodenum joins it at the right one. The pylorus does not project into the duodenum, and the sphincter is weak. The fundus is rugose. No gastric gland is present as in *Cœnolestes* (9), but there is a small lymphatic gland on the lesser curvature.

Text-figure 75.



The stomach in the Marsupialia. A. *Dendrolagus ursinus* open to show—*a*. central tract; *b*. sacculi; *c*. gland strips; *d*. œsophagus; *e*. pyloric region. B. *Perameles obesula*. C. *Metachirus opossum*. D. *Petaurus breviceps*. E. *Petaurus sciureus*.

The empty stomach of *Metachirus opossum* (text-fig. 75 C) differs from the above in the thickness of the pyloric region, the existence of well-marked rugæ on both walls, and the great strength of the pyloric sphincter. There is a small lymphatic gland on the lesser curvature as in *Perameles obesula*.

In *Petaurus sciureus* (text-fig. 75 E) the globular fundus is directed forwards and to the left. The duodenum, whose commencement is notched, leaves its dorsal aspect. In *P. breviceps* (text-fig. 75 D) the duodenum has no notches, but a groove marks the pyloro-duodenal junction. The greater curvature is sacculated.

In *Dendrolagus ursinus* (text-fig. 75 A)* the greater part is concealed by the liver, the only parts visible being the cardiac cul-de-sac and greater curvature. The form and general characters resemble those of other species already described by Beddard (**1**), Owen (**12**), and Carlsson (**2**). These authors compared the stomachs with those of other Macropodidæ, and described the extent of the glandular and non-glandular parts of the mucosa.

Owen and Beddard described groups of follicular glands lying along the sides of the central tract (*a*) in *D. inustus* and *D. bennetti.* In *D. ursinus* they are replaced by long glandular strips (*c*), into which branches of the abdominal parts of the vagus nerves can be traced, and the vagus branches probably contain sympathetic fibres. From the examination of the stomachs of animals belonging to most of the mammalian orders, I have come to the conclusion that the branches of the vagi are greatly increased in numbers when there is a special gastric glandular apparatus. These branches pass directly to the glands as in *D. ursinus*, or run through a plexus with ganglia as in *Phascolarctos cinereus* (**15**). The pylorus does not project into the duodenum in *Dendrolagus.*

Osgood described a special gastric gland in *Cœnolestes obscurus*, but did not mention its nerve supply.

The histology of the stomachs of the Marsupialia has already received considerable attention, and Oppel (**8**) has collected and analysed the various papers. I have nothing new to add to these accounts. Nematode worms are present in many stomachs.

The Intestinal Tract:—The observations recorded here are supplementary to those of Chalmers Mitchell (**6**, **7**), Cunningham (**3**), Owen (**10**), and Flower (**20**).

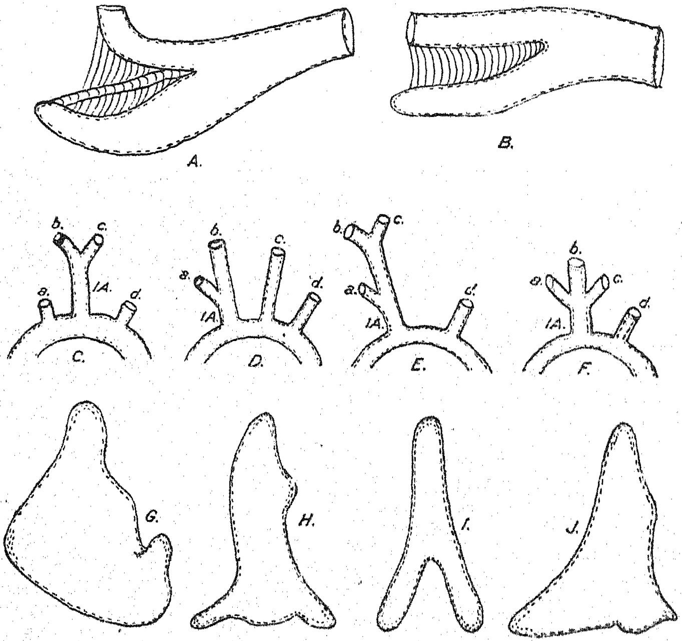
In *Metachirus opossum* the well-marked duodenal loop is wide, thin-walled, and extends posteriorly for a considerable distance. The flexure between its second and third parts is connected by the usual peritoneal ligament to the abdominal parietes and meso-colon, but is not continuous with the splenic ligament. The cæcum is two and a half inches long. It is capacious, and its interior is devoid of folds and septa. Meckel's Tract and the large intestine differ in no respect from that of *Didelphys virginiana* (**6**). The cæcal mesentery has a concave free edge and the angle between the cæcum and Meckel's Tract is bisected by an artery (text-fig. 76 A).

The cæcum of *Perameles obesula* (text-fig. 76 B) is one and three-quarter inches long. It is longer and thinner than that of *Peragale lagotis* figured by Chalmers Mitchell (6), and it has a mesentery whereas that of *P. lagotis* has not. In other respects the intestinal tracts of these Peramelidæ are similar. Their cæca differ from the minute conical appendage of *Cœnolestes obscurus* as figured by Osgood (9), and the latter is devoid of a mesentery.

---

* The specimen was specially hardened by injections of formalin to show the topography of the stomach.

Text-figure 76.



A. Cæcum of *Metachirus opossum*; B. cæcum of *Perameles obesula*; C–F. aortic arches with innominate (IA), right subclavian (*a*), right common carotid (*b*), left common carotid (*c*) and left subclavian (*d*) arteries; G–J. the spleens of the Marsupials (names in text).

The ligament running backwards from the duodenum in *Perameles obesula* crosses the front of the rectum and fuses with the splenic ligament. They enclose a pocket containing the rectum, and a probe passed into it runs backwards into the pelvis.

The intestinal tract of my nearly adult female *Dendrolagus ursinus* differs in several respects from that of a young specimen described by Chalmers Mitchell (7). The duodenal loop is sharply differentiated, but runs insensibly into Meckel's Tract. The coils of Meckel's Tract do not form a double spiral, and there is only one cæcum. The latter is fusiform, but is devoid of longitudinal bands, sacculi, and a vermiform appendage, and the superior mesenteric artery does not occupy the free edge of its mesentery. At the point where the ileum enters the colon there is a transverse vein. At a point two inches proximal to the ileo-cæcal junction there is a single Peyer's Patch measuring one and a quarter inches in length.

No trace of a second cæcum was found in my pouch specimens of *Macropus bennetti*, *Macropus giganteus*, *Onychogale lunata*, and *Bettongia penicillata*.

I have refrained from giving a detailed list of the measurements of the different parts of the intestinal tract in my specimens as they had been preserved for varying periods. The data, if given, would be of little value in consequence.

The Pancreas.

In all Marsupials examined except *Phascolarctos cinereus*, I found the pancreas much subdivided and dendritic, but the arrangements of the subdivisions varied considerably. In *Metachirus opossum* they are aggregated to form a compact mass in the posterior part of the duodenal loop, and a long, narrow part stretches across the abdomen to the spleen. Small branches are given off from the body. The duct opens into the duodenum along with the common bile-duct. *Perameles obesula* also possesses a long, narrow body with lateral processes, and the duodenal loop contains an almost complete ring of pancreatic tissue such as is found in some Rodents and Carnivora.

In *Petaurus sciureus*, *P. breviceps*, and *P. breviceps papuanus* the pancreas consists of long strips and small isolated pieces arranged along the course of the mesenteric vessels. It is difficult to detect the ducts of the small lobules, and it is impossible to do so when there is much fat in the omentum and mesentery. The same dendritic arrangement is seen in *Dendrolagus ursinus*, in which the pancreatic and common bile-ducts open separately into the duodenum. In *Macropus*, on the other hand, the ducts are confluent (Owen).

Osgood describes a dendritic pancreas in *Cœnolestes obscurus* (9), so its condition is no more highly evolved than that of *Perameles obesula*.

It is evident, therefore, that the pancreas of *Phascolarctos cinereus* is of a higher type than the dendritic, more or less diffuse, organ of other forms.

The Organs of Circulation.

The *Pericardium* adheres to the diaphragm in all Marsupials except *Trichosurus vulpecula*, and it adheres to a variable extent to the sternum and ribs. In *Dendrolagus ursinus* and pouch specimens of *Macropus giganteus* and *M. bennetti* the lungs were seen to overlap the base of the heart, and the precordia, or uncovered part, was adherent to the sternum and ribs.

The Heart:—In all Marsupials the apex is formed by the left ventricle, and the right ventricle falls short of it by a variable interval. Cunningham (**3**) states that the right ventricle in *Thylacinus* stops short of the apex by 1½ inches, but I never observed such a long interval in any Marsupial. In very young pouch specimens the right ventricle is relatively longer than in adults.

Owen (**11**) describes bifurcation of the right auricular appendix as one of the chief characteristics of the Marsupial heart, but some species have no trace of a division, and in others the division has no reference to the ascending aorta.

The appendix is conical and bifid in *Petaurus sciureus* and pouch specimens of *Macropus bennetti* and *Macropus giganteus*, but the two divisions are small. In *Dendrolagus ursinus* and *Perameles obesula* it is large and round; and the former has a well-marked process lying on the dorsal aspect of the aorta, but no trace is present in the latter. Cunningham pointed out that there is no bifurcation in *Thylacinus* and *Dasyurus*, but there is a strong division in *Cuscus* and *Trichosurus*. A slight division is present in *Phascogale*, but it has no reference to the ascending aorta (**3**). In *Phascolarctos cinereus* the secondary process is large, and the right precaval vein passes into it.

The characters of the interior of the auricles and ventricles of many Polyprotodonts and Diprotodonts have already been described by Cunningham.

The Aortic Arch:—In all Marsupials it describes a full curve and ends at the level of the fourth dorsal vertebra, and the relations are similar in all forms to those described in the Koala (**15**). The branches differ considerably, for six types are present, as shown in text-fig. 76 C–F.

1. Both carotids and subclavians arise separately, so no innominate artery is present—*Phascolarctos cinereus* †.
2. The two subclavian and the innominate arteries are given off, and the latter divides into the two common carotid arteries—*Dasyurus macrurus* (C).
3. The branches arise as in Man—*Phascolarctos cinereus* *, *Petaurus breviceps* *, and *Phascolomys mitchelli* (D).
4. The innominate artery gives off the left common carotid artery, and divides into the right subclavian and right common carotid arteries—*Trichosurus vulpecula* †.
5. The innominate artery gives off the right subclavian artery, and is continued as the bicarotid trunk which divides into the two common carotid arteries—*Thylacinus harrisi*, *Didelphys cancrivora*, *Dasyurus viverrinus*, and *Petaurus australis* * (E).
6. The innominate artery gives off the right subclavian and both common carotid arteries at the same level—*Cuscus maculatus*, *Dendrolagus ursinus*, *Phascolarctos cinereus* *, and *Macropus giganteus* (F).

* These observations are recorded in hitherto unpublished notes by Garrod.

† These types have been figured in my paper on the Koala.

The left subclavian artery is the only constant branch, and the left superior intercostal artery sometimes arises from the arch a little distal to it.

I agree with Cunningham that there is no trace of the obliterated ductus arteriosus. And I have nothing to add to existing descriptions of the remainder of the arteries.

The *Vena Transversa* is usually horizontal and drains the mouth, tongue, salivary glands, and some of the cervical muscles. In a few cases it receives laryngeal veins. In some specimens of *Trichosurus vulpecula* it is connected to the internal jugular veins by vessels corresponding to the anterior jugular veins of the Ocelot and Man. I have already figured these in my paper on the Koala and Vulpine Phalanger (**15**).

The *External Jugular Veins* in all Marsupials are similar to those described in my paper on the Koala.

In all Marsupials examined by me there are two *precaval veins*, but Garrod mentions in a hitherto unpublished note that the two innominate veins unite about half an inch in front of the heart to form a single precaval vein in *Petaurus breviceps*.

The *Postcaval Vein* covers the posterior half of the abdominal aorta in all Marsupials examined by me except *Phascolarctos cinereus*, and Hochstetter found it covering the aorta in all except *Petaurus taguanoides*. Beddard found it covering the aorta in all his specimens.

The Urinary Organs.

The *kidneys* are conglobate in all Marsupials, and their relative positions vary as follows:—

1. Right kidney entirely anterior to the left one—*Phascolarctos cinereus*.
2. Posterior pole of right kidney level with the hilum of the left one—*Metachirus opossum*, *Marmosa elegans*, *Perameles obesula*, *Petaurus sciureus*, and *Trichosurus vulpecula*.
3. Both kidneys situated at the same level—*Macropus giganteus*, *Macropus bennetti*, *Dendrolagus ursinus*, and *Cœnolestes obscurus*.

On section only one papilla is present, and it may be sharp and conical, or broad and flat. Small nodule-like elevations may be present on broad, flat papillæ. No fat is present in the kidney pelves in any of my specimens.

The course of the *ureters* is similar to that already described in my paper on the Koala and Vulpine Phalanger (**15**).

Tha ventral surface of the bladder is connected to the ventral abdominal wall by a ligament, which varies in prominence in different species. It is thin in the Polyprotodonts and thick in *Dendrolagus ursinus*. In that species, as in *D. bennetti* (**1**), its attachment to the abdominal wall is very extensive. In all species it is completely anangious. It represents the remains of the ventral mesentery. Lateral vesical ligaments are absent.

The dorsal surface of the bladder of *Dendrolagus ursinus* is connected to the dorsal abdominal wall at the sides of the vertebral column by two strong ligaments, which divide the pelvic cavity into a median and two lateral compartments. The central one contains the rectum and uterus, and the oviducts curl over the free edges of the ligaments.

In *Perameles obesula* the uterus is separated from the rectum by the wall of the peritoneal pocket formed by the fusion of the splenic and duodenal ligaments.

I have nothing to add to the existing descriptions of the generative organs of either sex, nor to Osgood's *résumé* of our knowledge of the marsupial bones (**9**). In the latter paper the nipples are also enumerated, and it is shown that they are asymmetrically arranged in the Didelphyidæ alone.

The Ductless Glands.

The *suprarenal capsules* are situated on the mesial aspects of the anterior poles of the kidneys in all Marsupials examined by me except *Phascolarctos cinereus*, and that species has a very prominent ligament uniting the left kidney and its capsule.

The Thymus Gland.

The Polyprotodonts differ from the Diprotodonts in the characters of the thymus gland. In the former it consists of two elongated or oval bodies in the anterior part of the thorax, but in the latter there are two cervical lobes in addition; and one must be careful to distinguish them from salivary glands. Osgood (**9**) found four thoracic glands in *Cœnolestes*.

Topography:—The cervical lobes lie immediately under cover of the platysma. They are oval or pyriform, with the narrow ends turned forwards. They lie at the root of the neck, as in *Dendrolagus ursinus* (text-fig. 74 B), *Macropus giganteus* (text-fig. 71, *k*), and *Macropus rufus*, or they may extend far forwards and even conceal one of the submaxillary glands, as in *Petaurus sciureus* (text-fig. 73, *k*). They may touch the parotid glands anteriorly, or be in contact with them throughout the entire length of the neck as in *Trichosurus vulpecula*. In *Pseudochirus peregrinus* they are concealed by the parotid glands. They may be in contact with the mid line, or an interval in which the pretracheal muscles are seen may separate them. The subjacent structures are the sterno-mastoids, pretracheal muscles, and part of the sternum and clavicles.

The surfaces may be finely or coarsely lobulated, and in no case were they invested by a connective-tissue capsule derived from the cervical fascia.

Symington (**17**) described and figured the topography of the thoracic lobes, and described the gland in a number of Marsupials. His observations on the Polyprotodonts are limited to *Didelphys virginiana* and *Dasyurus cancrivora*. He could not detect cervical lobes in either of these species, and I was unable to detect them in the Didelphyidæ, Dasyuridæ, and Peramelidæ. He believes that the primitive condition is present in the Dasyuridæ, and the cervical lobes of the Diprotodonts are a specialization in association with the vegetable diet and the call for a larger amount of thymic tissue. If, as Swale Vincent suggests, the cervical and thoracic lobes perform different functions, it is difficult to ascribe any use other than dietetic to the former.

As age advances, the thymus—both cervical and thymic—diminishes in size and degenerates.

The Thyroid Gland.

In *Perameles obesula* the left lobe is long and narrow, but the right one is short and oval, and partly under cover of the pectoralis major. No isthmus is present; and this arrangement is the reverse of that which I have already described in *Phascolarctos cinereus* (**15**).

In all other Marsupials, I found the gland to be composed of two small, oval lobes lying on the sides of the larynx alone (*Petaurus sciureus*), or the posterior part of the larynx and a variable number of tracheal rings; and the only animal possessing an isthmus is *Trichosurus vulpecula*.

Each lobe receives a single artery from the common carotid, and the veins join the internal jugular veins.

The lobes were concealed by the pretracheal muscles in all animals examined except a male pouch specimen of *Macropus giganteus*.

The Spleen (text-fig. 76 G–J).

The observations recorded here are supplementary to those of Colin Mackenzie (**5**), Owen (**11**), and Retterer (**21**).

In most genera there is little variation in form in the various species, but the spleen has different shapes in the species of *Dendrolagus*. In *D. ursinus* it is long and **Y**-shaped, with rounded extremities (text-fig. 76 I). In *D. inustus* (**12**) it is **T**-shaped, and it is spoon-shaped in *D. bennetti* (**1**). Carlsson (**2**) states that it is pointed in *D. dorianus*.

In *Petaurus sciureus* (text-fig. 76 J), *P. breviceps*, and *P. breviceps papuanus* the spleen is triangular, with sharp angles not prolonged into processes, and the base of the triangle is applied to the greater curvature of the stomach.

The spleen of *Phalanger orientalis* resembles those of the Petaurists, the only difference being that its apical angle is 90°, whereas those of the latter are larger.

Colin Mackenzie described and figured the spleen of *Macropus* and my specimens differ in no way from his description; and a pouch specimen of *Onychogale lunata* has a **Y**-shaped spleen similar to that of the Kangaroos. The form does not alter from birth to adult life.

In *Perameles obesula* (text-fig. 76 G) the spleen has a massive triangular body with thick sides, and the angles are prolonged by cylindrical or flattened processes of splenic tissue. If the processes are removed, the resulting organ resembles that of *Phascolomys* described and figured by Colin Mackenzie. Garrod states in a hitherto unpublished note that the spleen of the Wombat forms an equilateral triangle. In a specimen of *Phascolomys mitchelli* it had a lateral piece. In *Perameles nasuta* it is thin and triangular, without prolongations.

The Bandicoots are the only Marsupials in which I observed a continuity between the splenic and duodenal peritoneal ligaments. And the looseness of connection between the spleen and stomach differs considerably; these viscera were very closely united to one another in *Dendrolagus ursinus*.

Osgood (9) showed that the spleen of *Cœnolestes obscurus* has an elongated body and a lateral piece, so it differs from that of *Perameles obesula*.

In *Metachirus opossum* it is T-shaped, with one of the horizontal limbs short (text-fig. 76 H).

The external appearances of the spleens differ considerably even in different species. Histological examination of the spleens of many Marsupials shows that there is a very strong trabecular network.

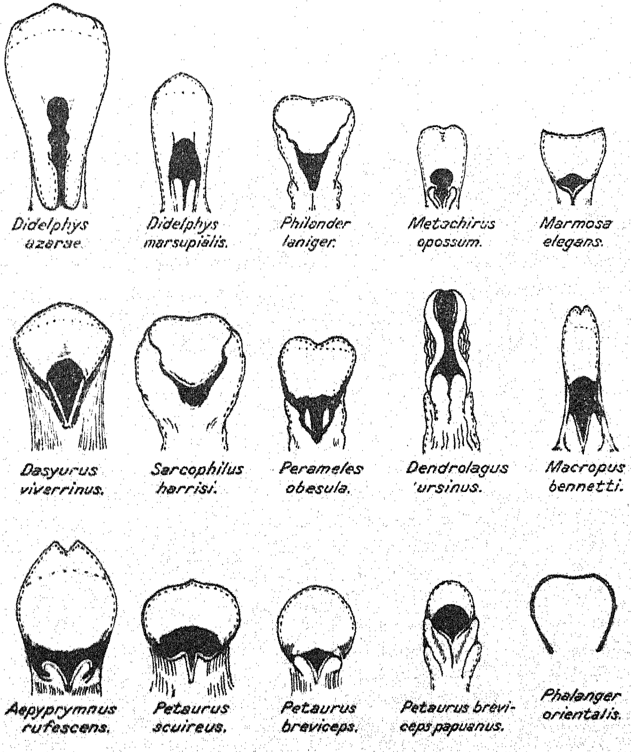
The Respiratory Organs.

The *epiglottis* is large, and its apex, which is entire or notched, is frequently emarginate. It lies vertically or inclined forwards, and it is sometimes gripped by the posterior extremity of the nasal tube. And it is closely related to the base of the tongue in all Marsupials except *Phascolarctos cinereus*. As the form of the epiglottis and prominence of the aryteno-epiglottic folds vary, the shape and size of the superior aperture of the larynx differ considerably (text-fig. 77).

In *Didelphys azaræ* the epiglottis is large, conical, connected to the arytenoids by prominent ligaments, and strongly emarginate, without any trace of a notch. The superior aperture of the larynx is long and narrow, and cuts into the posterior surface of the epiglottis. In *D. marsupialis*, on the other hand, the entire epiglottis is only slightly emarginate, the arytenoid cartilages are plainly visible, and the superior laryngeal aperture is wide and round. In *Philander laniger* and *Marmosa elegans* the epiglottis is broad, and its apical margin is slightly concave but not emarginate; and the superior aperture of the larynx is triangular. Their condition is intermediate between those of *Didelphys* and *Metachirus opossum*, in which the non-emarginate apex of the epiglottis is notched. The epiglottis, therefore, is of considerable value for differentiating the genera of the Didelphyidæ from one another.

The epiglottis is large, prominent, and entire in the Dasyuridæ. In *Dasyurus viverrinus* it is uniformly thick and the apex is slightly emarginate. Its connections to the arytenoid cartilages are also thick, and the superior aperture of the larynx is large and open. The rima glottidis has very thick boundaries. In *Sarcophilus harrisi*, on the other hand, the epiglottis is large and thin, and its posterior parts are folded inwards and lean against the anterior parts, so the superior aperture of the larynx is a transverse slit. And the arytenoid cartilages and rima glottidis are entirely concealed.

Text-figure 77.



The larynx of the Marsupialia. The convex dotted lines crossing the epiglottis are the levels of emargination.

The epiglottis of *Perameles obesula* has a broad, emarginated, notched apex; and there is a small fossa with a crescentic orifice between the epiglottis and the tongue. The characters of the fossa in *P. lagotis* have already been described by Owen (**10**).

In the Macropodidæ there is considerable variation in the characters of the epiglottis. In *Dendrolagus ursinus* it is entire and the sides are folded inwards, so the superior laryngea aperture has the form of the figure 8, and the rima glottidis is invisible. In *Æpyprymnus rufescens*, *Macropus bennetti*, and *Macropus giganteus* the apex of the prominent epiglottis has a small sharply-cut notch resembling that in *Trichosurus vulpecula*, and much emargination is present. The notches in the Polyprotodont, on the other hand, are wider and shallower.

Owen (**10**) states that the epiglottis of the Phalangers is broad and bifid, but I found it entire and slightly concave in a mammary fœtus of *Phalanger orientalis*. It is entire in *Pseudochirus peregrinus*, *Petaurus sciureus*, *Petaurus breviceps*, and *Petaurus breviceps* var. *papuanus*. In *Petaurus sciureus* the degree of emargination is considerable.

The large entire epiglottides in *Phasolarctos cinereus* (**15**) and *Cœnolestes obscurus* (**9**) have already been described.

The characters of the other cartilages, and the cords, ventricles, and muscles are described by Owen.

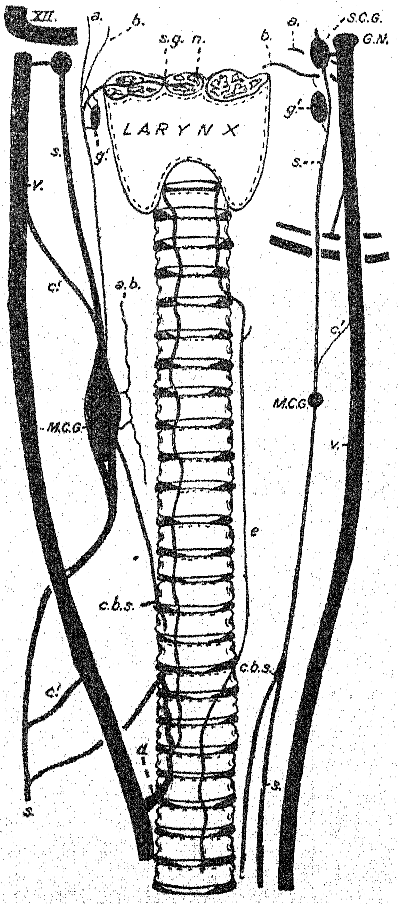
The *trachea* is usually long and narrow, but it is short and wide in *Phascolarctos cinereus*. The cartilages frequently form complete rings, but in many species they are defective behind and a membrane fills the gap. Some of the rings are expanded and thickened on one side, and the numbers observed were:—*Metachirus opossum* 19; *Perameles obesula* 34; *Petaurus sciureus* 35; *Dendrolagus ursinus* 35. The numbers in other Marsupials have been recorded by Cunningham (**3**), Osgood (**9**), and Owen (**10**). In Marsupials in which the vagus and sympathetic are separate, the tracheal and pulmonary plexuses are large.

The Lungs:—My observations differ from those of Owen (**10**) in a number of cases. In the Didelphyidæ the right lung is trilobate and has a well-marked azygos lobe. The left lung is entire in *Metachirus opossum*, but is bilobate in *Marmosa elegans*. In *Perameles obesula* the right lung has three lobes and an azygos appendage, and the left one is entire; Owen also states that the left lung of *Perameles* is undivided. The Phalangeridæ have bilobate left lungs, and the right ones are trilobate with the azygos lobe in addition. In the Macropodidæ, of which *Dendrolagus ursinus*, *Macropus bennetti*, and *Macropus giganteus* were examined, both lungs have deep median sulci dividing them into anterior and posterior parts, but these are not entirely separated from one another, and the azygos lobe is large. The conditions differ from those of other Kangaroos described by Owen (**10**). The mesial borders of the lungs are thin in the Macropodidæ.

The division of the lungs appears to differ considerably even in the same species. Osgood (**9**) observed variations in *Cœnolestes obscurus*, and Owen, Forbes, and I have recorded three different arrangements in *Phascolarctos cinereus*. I am unaware of any account of the lobes of the lungs of the uterine fœtus, and it is important to ascertain whether there is fusion of lobes of the left lung during development similar to that which takes place in *Bradypus tridactylus*, in which the fœtal lungs are divided into lobes; but those of the adult are entire.

In a *Dendrolagus ursinus* hardened by formalin injections it is seen how the lungs conceal the large vessels and part of the right auricular appendix.

Text-figure 78.



The cervical parts of the vagi and sympathetics in *Dendrolagus ursinus*. Letters in text.

The Vagus and Sympathetic Nerves[*].

No account of the viscera of any animal is complete without a description of these nerves, which control their activities.

The cervical parts are arranged in two ways in the Marsupialia.

---

[*] The lettering on text-figs. 78 and 79 corresponds, so far as possible, to that of text-figs. 62 and 63 in my paper on the Koala (**15**).

In the first type, which is present in both Polyprotodonts and Diprotodonts, they are fused to form vago-sympathetic cords. In the second form, which is found only in Diprotodonts, they are connected by a variable number of communicating branches. In no Marsupial did I find both types present in the neck as I observed them in *Tamandua tetradactyla* and *Lutra maculicollis*. These forms were present as follows in my specimens:—

Type 1:—*Metachirus opossum*, *Didelphys azaræ*, *Didelphys marsupialis*, *Philander laniger*, *Dasyurus viverrinus*, *Sarcophilus harrisi*, *Perameles obesula*, *Phascolarctos cinereus*, *Trichosurus vulpecula*, and *Petaurus sciureus*.

Type 2:—*Dendrolagus ursinus*, *Macropus giganteus*, *Macropus bennetti*, *Pseudochirus peregrinus*, and *Æpyprymnus rufescens*.

The course of the vagi from the base of the skull to the point where they reach the œsophagus in the posterior part of the thorax has already been described in my paper on the Koala (**15**), but the branches vary considerably.

The vagus (V) and hypoglossal (XII) nerves are fused in *Phascolarctos cinereus*, but branches of communication run between them in other Marsupials.

In *Dendrolagus ursinus* the pharyngeal (*a*) and superior laryngeal (*b*) nerves are given off from the sympathetic on the right side, but from the vagus on the left. The cord giving off the right nerves supplies the submaxillary glands (*s.g.n*), and possesses a ganglion (*g'*); it probably contains vagus fibres.

The vagus and sympathetic communicate. In the first type branches run between the vagus and superior cervical ganglion (*s.c.g*). In the second type there are several branches of communication (*c'*) throughout the neck as well.

At the root of the neck the right vagus gives off its recurrent branch (*d*), and the vago-sympathetic cord is resolved again into its component vagus (*v*) and sympathetic (*s*) elements. I observed no communications between the right and left recurrent laryngeal nerves, but the right nerve and sympathetic cord communicated.

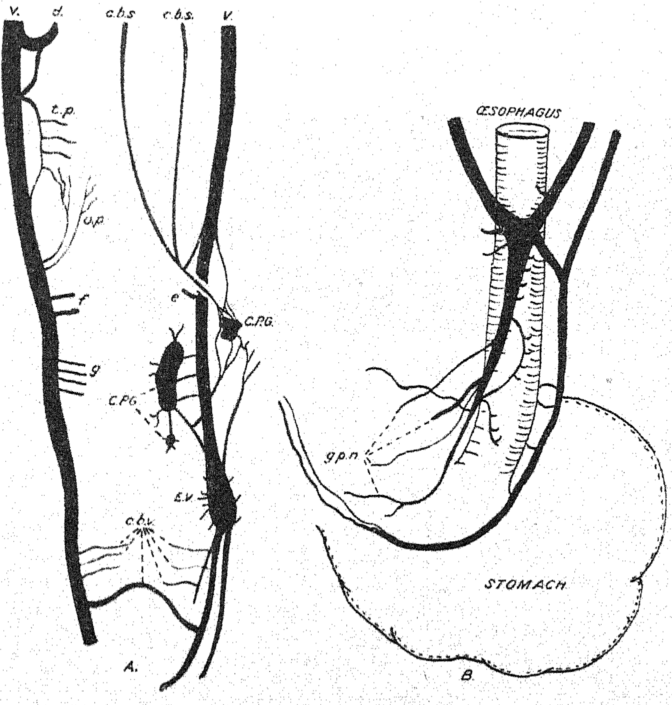
Cardiac Nerves:—In type 1 the vagus transmits sympathetic cardiac nerves, but in type 2 (text-fig. 79) the cardiac branches of the vagus (*f*) and sympathetic are separate throughout. And the cardiac branches of the sympathetic (*c.b.s*) come from the middle ganglion or main cord, but never from the superior ganglion. The cardiac and pulmonary plexuses have well-marked ganglia in *Dendrolagus ursinus*, and that species has large tracheal and œsophageal plexuses.

The Posterior Thoracic Parts of the Vagi:—In the Koala, as in some reptiles, birds, and Man (Wirsung's case), they are fused to form a combined trunk; but the trunk of the Koala is not resolved again into the two vagi. And many gastric nerves are given off in the thorax.

In *Metachirus opossum* the left vagus runs along the ventral surface of the œsophagus. It gives off a branch which accompanies the right vagus on the dorsal aspect on the œsophagus. And no branches of communication run between the vagi*. In *Perameles obesula* the cords have a similar disposition, but communicating branches run between them.

The conditions are more complex in *Dendrolagus ursinus* (text-fig. 79 A). The vagi are linked together by numerous branches of communication (*c.b.c*). The left one has a large oval expansion (EV) beyond which it bifurcates, and the right half fuses with the right vagus. The branches of supply to the œsophagus are very numerous.

Text-figure 79.



The vagus and sympathetic in *Dendrolagus ursinus*. A. In anterior two-thirds of thorax. B. Posterior thoracic and abdominal parts. *op*. œsophageal plexus; *tp*. tracheal plexus; *f*. right cardiac branches of vagus; *g*. pulmonary nerves; C.P.G. ganglia of cardiac and pulmonary plexuses. Other letters in text.

In no case did I find any communication between the vagus and phrenic nerves.

Abdominal Parts of the Vagi:—The vagi terminate in three ways in the Marsupialia. The combined trunk ends in the solar plexus, and gives branches to the stomach in the Koala as in some lower Vertebrata. In *Metachirus opossum* and *Perameles obesula* the left vagus ends in the ventral wall of the stomach, and the right one gives branches to the stomach and ends in the solar plexus. In the third type, which is exemplified by *Dendrolagus ursinus* (text-fig. 79 B), the main masses of the vagi end in the stomach, and branches of communication run to the solar plexus. Numerous branches (*g.p.n*) run to the special gastric gland.

---

* In *Nandinia binotata*, the most primitive Carnivore, the conditions resemble those in *Metachirus*.

I never observed any other mode of termination in the Mammalia, but the branches of communication between the vagi and the abdominal sympathetic plexus are more numerous in some of the Eutheria.

The Cervical Sympathetic:—The arrangement in animals with the first type is figured in my paper on the Koala (**15**), and that in the second type is shown in text-fig. 78.

The superior cervical ganglion (S.C.G) is always present; the inferior one is frequently present, but the middle one (M.C.G) is very variable. It is well-marked in *Dendrolagus ursinus*, but absent in *Æpyprymnus rufescens*. In a pouch specimen of *Macropus giganteus* it appears as a slight increase in the diameter of the nerve. When both middle ganglia are present one may be minute and give off no branches. The branches of the cervical sympathetic are:—

1. Communicating to the cervical plexuses, vagi, and right recurrent laryngeal nerve.
2. Branches accompanying the common carotid (*a.b*), subclavian, and vertebral arteries.
3. Cardiac nerves (*c.b.s.*) which arise from the middle or inferior ganglia or main cords themselves.

I was unable to trace the filaments accompanying the vertebral arteries to the brain. In some higher Mammals they can be traced nearly to the interpeduncular space.

The sympathetic cords terminate in one of three ways. They may end in the solar plexus and give off no branches to the aortic plexus; and in this and the next form no splanchnic nerves are present. In the second type the main mass of the sympathetic ends in the solar plexus, but sends a small communication branch to the aortic plexus. In the third type, which is the commonest, the cords run back to the sacral region, and splanchnic nerves are present.

It has been shown by Volkmann, Bidder, and others that the sympathetic becomes included more and more in the vagus as we descend the vertebrate scale, and I believe that the form in which they are fused in the neck is more primitive than that in which they are separate. The nerves are fused in the neck in *Ornithorhynchus* (Knox).

In *Dendrolagus ursinus* the phrenic nerves bifurcate beyond the roots of the lungs, and the halves pass to the ventral and dorsal parts of the diaphragm. The nerve to the omo-hyoid comes from the cervical plexus, and has no connection with the hypoglossal nerve as in *Petrogale xanthopus*.

Systematic.

When the structures described above are arranged in systematic order, the following results are obtained:—

Sub-order POLYPROTODONTIA.

Characters common to all Genera:—Lips entire. Both frenums present. Three circumvallate papillæ, a well-developed sublingua, and no lateral organs. Tonsils compact. Stomach simple and has no special gland. Parotids small. Submaxillaries large. Intestinal tract short. No cervical thymus. No thyroid isthmus. Post-caval vein covers aorta. Vagus and sympathetic fused.

Family DIDELPHYIDÆ.

Characters common to all Genera:—Oral vestibule smooth. No cheek-pouches. Duodenal loop differentiated. Cæcum well-developed. Thyroid gland anterior. Mammæ asymmetrical. Patella not ossified.

Genus *Didelphys*:—Labial tubercles variable. Palatal formula C_9I_1P+U-. Epiglottis conical, entire, emarginate. Lower œsophagus transverely rugose. Mammæ 5–13.

Genus *Metachirus*:—No labial tubercles. Palatal formula C_8I_0P-U-. Epiglottis notched. Lower œsophagus not transversely rugose. Mammæ 7–9.

Genus *Philander*:—No labial tubercles. Palatal formula C_8I_1P+U-. Epiglottis has concave anterior border and rounded angles. Lower œsophagus not transversely rugose. Mammæ 7.

Genus *Marmosa*:—No labial tubercles. Palatal formula C_9I_0P-U-. Epiglottis with concave anterior border and sharp angles. Lower œsophagus not transversely rugose. Mammæ 9–15.

Family DASYURIDÆ.

Characters common to all Genera:—No cheek-pouches. Duodenal loop not differentiated. Cæcum absent. Thyroid gland anterior. No transverse œsophageal rugæ. Mammæ symmetrical. Patella not ossified.

Genus *Dasyurus*:—Labial tubercles opposite canine teeth. Oral vestibule papillose. Palatal formula C_8I_8P+U-. Epiglottis thick, rounded, entire. Mammæ 6–8.

Genus *Sarcophilus*:—No labial tubercles. Oral vestibule smooth. Palatal formula C_7I_8P+U-. Epiglottis thin and parts crushed together. Mammæ 4.

Family PERAMELIDÆ.

Genus *Perameles*:—No labial tubercles. Oral vestibule with hard ridges. Cheek-pouches (?) small fossæ. Palatal formula $C_{11}I_8P+U-$. Epiglottis notched. No transverse œsophageal rugæ. Duodenal loop differentiated. Cæcum well-developed. Spleen massive and triangular. Thyroid gland posterior. Mammæ symmetrical. Patella ossified. Mammæ 6–8.

Sub-order DIPROTODONTIA.

The Diprotodontia have few characters common to all their genera in contradistinction to the Polyprotodontia. And these characters are:—Parotid glands large. Tongue has reduction in the sublingua and shows lateral organs. Thymus gland has two cervical and two thoracic lobes. Meckel's Tract long. Cæcum large.

Family MACROPODIDÆ.

Characters common to all Genera:—Lips cleft. No cheek-pouches. Oral vestibule ridged. Œsophagus has no transverse rugæ. Stomach sacculated. Lungs have small degree of division. Vagus and sympathetic nerves separate. Thyroid gland anterior and has no isthmus. Mammæ symmetrical. Patella not ossified.

Genus *Macropus*:—Both labial frenums present. Palatal formula C_8I_0P+U-. Epiglottis notched and wide. Spleen with lateral process. Stomach has patches of follicular glands and the area of digestive epithelium is small. Œsophagus enters stomach near cardiac end. Mammæ 4.

Genus *Dendrolagus*:—Large labial tubercles. No lower labial frenum. Palatal formula C_8I_0P+U-. Epiglottis entire and folded. Stomach with large area of digestive epithelium and follicular glands in patches or strips. Spleen Y-, T-, or spoon-shaped. Œsophagus enters stomach near cardiac end. Mammæ 4.

Genus *Epyprymnus*:—No labial tubercles. Both labial frenums present Palatal formula C_7I_0RU-. Epiglottis wide and notched. Œsophagus enters stomach near pyloric end.

Family PHALANGERIDÆ.

Characters common to all Genera:—Lips entire. No cheek-pouches. Œsophagus has no transverse rugæ. Stomach simple and has no special gland. Duodenum not a very specialized loop. Meckel's Tract short. Cæcum well-marked. Mammæ symmetrical. Patella not ossified.

Genus *Petaurus*:—No labial tubercles. Both labial frenums present. Oral vestibule smooth. Palatal formula varies. Epiglottis entire and rounded. Spleen an isosceles triangle. Vagus and sympathetic fused. Mammæ 4.

Genus *Pseudochirus*:—Lower labial frenum absent. Large labial tubercles. Oral vestibule ridged. Palatal formula C_8I_0P-U-. Epiglottis entire. Vagus and sympathetic separate. Mammæ 4.

Genus *Phalanger*:—Both labial frenums present. No labial tubercles. Oral vestibule smooth. Palatal formula C_9I_0P+U-. Epiglottis with shallow notch. Spleen a rectangular scalene triangle. Vagus and sympathetic fused. Mammæ 4.

Genus *Trichosurus*:—Both labial frenums present. Labial tubercles present. Oral vestibule smooth. Palatal formula C_8I_0P-U-. Epiglottis with sharp notch. Spleen with lateral piece. Vagus and sympathetic fused.

Family PHASCOLARCTIDÆ.

Genus *Phascolarctos*:—Both labial frenums present. No labial tubercles. Oral vestibule papillose. Palatal formula C_9I_0TU-. Epiglottis large, entire, emarginate. Spleen an isosceles triangle. Stomach has a special gastric gland. Vagus and sympathetic fused. Mammæ 2 and are symmetrical. Patella absent.

Osgood (9) described the resemblances between *Cœnolestes obscurus* and modern Peramelids, and the following table shows the differences between it and *Perameles obesula*:—

Perameles obesula.	*Cœnolestes obscurus.*
1. Four large follicles in the submental triangle.	1. Absent.
2. Platysma and panniculus strong.	2. Weak.
3. Digastric muscular and less extensive.	3. Digastric has aponeurotic attachment between symphysis menti and mandibular angle.
4. Palatal formula $C_{11}I_5P+U-$.	4. Formula C_9I_5P+U-.
5. Absent.	5. Labial labrets present.
6. Epiglottis notched.	6. Entire.
7. No special gastric gland.	7. Present.
8. No precardial lymphatic gland.	8. Present.
9. Parotid glands small.	9. Large.
10. Sublingual glands small.	10. Large.
11. Cheek-pouches minute.	11. Large.
12. Two thoracic thymic lobes.	12. Four thoracic thymic lobes.
13. Spleen triangular.	13. Spleen with lateral piece.
14. Thyroid gland in posterior part of neck.	14. In anterior part.
15. Well-marked cæcal mesentery.	15. Absent.
16. Lower pole of right kidney level with hilum of left one.	16. Kidneys at same level.
17. Mammæ 8.	17. Mammæ 4.
18. Large marsupium in adult.	18. Marsupium absent in adult and rudimentary in the young.
19. Arterial canal of seventh cervical vertebra incomplete.	19. Complete.

In my paper on the Koala and Vulpine Phalanger I tabulated the differences between them, and stated that the Phalanger has characters possessed in common by many Marsupials. The following list enumerates the points in which all forms differ from *Phascolarctos cinereus*:—

1. Hyoglossus muscle present.
2. Vena transverse horizontal.
3. Anterior palatal ridges convex forwards.
4. Tongue close to epiglottis.
5. Pylorus does not project into duodenum.
6. Tonsils in fauces.
7. Pharynx has no dorsal ridges.
8. Innominate artery present.
9. Postcava covers abdominal aorta.
10. Gall-bladder does not extend as far as the middle of the duodenum.
11. Pancreas dendritic.
12. Patella present.
13. Right lung has an azygos lobe.

I have nothing new to add to the well-known external and skeletal characters of the Marsupialia.

Summary and Conclusions.

1. The mylo-hyoid and sterno-hyoid muscles are attached to the hyoid bone, and the hyoglossus muscles are present in all Marsupials except *Phascolarctos cinereus*.

2. The sterno-facialis muscle may arise from the platysma by splitting.

3. The characters of the mouth and epiglottis are very variable in the Marsupialia, and I would urge that they be added to those at present in use for purposes of classification.

4. The right auricular appendix is not always bifid, as stated by Owen, and sometimes the division has no relation to the ascending aorta.

5. When a special gastric gland is present, the abdominal branches of the vagi are very numerous.

6. The Polyprotodonts have small parotids and large submaxillaries, but the reverse is the case in Diprotodonts. The largest glands are present in *Dendrolagus*.

7. The thyroid isthmus and anterior jugular veins are only found in *Trichosurus vulpecula*.

8. The postcaval vein covers the aorta in all Marsupials except *Phascolarctos cinereus* and *Petaurus taguanoides*.

9. The vagus and sympathetic nerves are fused in the neck in all Polyprotodonts and some Diprotodonts, but they are separate in a few Diprotodonts. From the examination of these nerves in all classes of vertebrates I have come to the conclusion that the former is the more primitive type.

10. The Polyprotodonts have more characters common to all genera than the Diprotodonts. And they retain primitive characters in their tongues, intestinal tracts, thymus glands, and nervous systems.

BIBLIOGRAPHY.

1. BEDDARD, F. E.—"The Visceral Anatomy and Brain of *Dendrolagus bennetti.*" Proc. Zool. Soc. Lond. 1895, pp. 131–137.
2. CARLSSON, A.—"Über *Dendrolagus dorianus.*" Zool. Jahrb. Jena, Systematik, xxxvi. pp. 547–617. 1913–14.
3. CUNNINGHAM, D. J.—'Challenger' Reports. Zool., V., pt. xvi. pp. 1–192. 1882.
4. GARROD, A. H.—"On the Kangaroo called *Halmaturus luctuosus* by d'Albertis, and its Affinities." Proc. Zool. Soc. Lond. 1875, pp. 48–59.
5. MACKENZIE, COLIN.—Journal of Anatomy and Physiology, 1916, pp. 1–18.
6. MITCHELL, P. CHALMERS.—"On the Intestinal Tract of Mammals." Trans. Zool. Soc. Lond. xvii. pt. v. pp. 437–535. 1905.
7. MITCHELL, P. CHALMERS.—"Further Observations on the Intestinal Tract of Mammals." Proc. Zool. Soc. Lond. 1916, pp. 190–199.
8. OPPEL, A.—Lehrbuch der verg. mikr. Anat. vols. i.–iii.
9. OSGOOD, W.—"A Monographic Study of the American Marsupial *Cænolestes.*" Field Museum of Nat. Hist., Zool., Chicago, May 1921.
10. OWEN, R.—The Comparative Anatomy of Vertebrates, vol. iii.
11. OWEN, R.—Art. "Marsupialia" in Todd's 'Cyclopædia of Anatomy and Physiology,' vol. iii.
12. OWEN, R.—"Notes on the Anatomy of the Tree-Kangaroo (*Dendrolagus inustus* Gould)." Proc. Zool. Soc. Lond. 1852, pp. 103–108.
13. PARSONS, F. G.—"On the Anatomy of *Petrogale xanthopus*, etc." Proc. Zool. Soc. Lond. 1896, pp. 683–714.
14. POULTON, E. B.—"On the Tongues of the Marsupialia." Proc. Zool. Soc. Lond. 1883, pp. 599–628.
15. SONNTAG, C. F.—"The Comparative Anatomy of the Koala and Vulpine Phalanger." Proc. Zool. Soc. Lond. 1921, pp. 547–577.
16. SWAN, J.—The Comparative Anatomy of the Nervous System of Vertebrates. 1864.
17. SYMINGTON, J.—"The Thymus Gland in the Marsupialia." Jour. Anat. Phys. xxxii. pp. 278–291. 1898.
18. SWALE, VINCENT.—Internal Secretion and the Ductless Glands. London, 1912, pp. 353–366.

19. Windle, B., & Parsons, F.—"On the Anatomy of *Macropus rufus*." Jour. Anat. Phys. xxxii., N. S. xii. pp. 119–134. 1898.
20. Flower, W. H.—"On the Organs of Digestion in Mammalia." Medical Times and Gazette, 1872, pp. 645–647.
21. Retterer.—C. R. Soc. Biol. vol. 78, p. 535. 1915.

The papers by Carlsson, Osgood, and myself contain extensive bibliographies. Owen's article on the Marsupialia in Todd's 'Cyclopædia of Anatomy and Physiology' enumerates the older papers. The external characters of the Diprotodonts have been described by Pocock, P. Z. S. 1921, pp. 591–608.

EXHIBITIONS AND NOTICES.

October 18th, 1921.

Sir S. F. HARMER, K.B.E., Sc.D., F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the months of May, June, July, August, and September, 1921:—

MAY.

The registered additions to the Society's Menagerie during the month of May were 307 in number. Of these 60 were acquired by presentation, 206 were deposited, 18 were purchased, 11 were received in exchange, and 12 were born in the Menagerie.

The following may be specially mentioned:—

2 Cheetahs (*Cynælurus jubatus*), ♀, from Hargeisa, Somaliland, presented by Major E. H. Ward, R.M.A., and Lieut. A. M. Hutchinson on May 30th.

2 Tayras (*Galera barbara*) and 1 Kinkajou (*Potos caudivolvulus*), from Ambalema, Colombia, presented by Henry C. Vaughan on May 17th.

4 Crab-eating Dogs (*Canis thous*) and 2 White Amphisbænas (*Amphisbæna alba*), from Morro Velho, Brazil, presented by George Chalmers, C.M.Z.S., on May 23rd.

2 Small Egyptian Jerboas (*Jaculus jaculus*) from Giza, 2 Large Egyptian Jerboas (*Jaculus orientalis*), from Maryût, and 2 Four-toed Jerboas (*Scarturus tetradactylus*), new to the Collection, from Maryût, presented by the Giza Zoological Gardens on May 21st.

JUNE.

The registered additions to the Society's Menagerie during the month of June were 399 in number. Of these 167 were acquired by presentation, 123 were deposited, 11 were received in exchange, 52 were purchased, and 46 were born in the Menagerie.

The following may be specially mentioned:—

2 young Lionesses (*Felis leo*) and one Bull Buffalo (*Bos caffer*), from Naorobi, presented by Maj.-Gen. Sir E. Northey, K.C.M.G., on June 7th.

A collection of Mammals from Burma, including a pair of Thamin (*Cervus eldi*), a pair of Hog-Deer (*Axis porcinus*), a pair of Muntjac (*Muntiacus muntjak*), a Tigress (*Felis tigris*), and two Burmese Pig-tailed Macaques (*Macacus leoninus*), received in exchange from the Rangoon Zoological Gardens on June 25th.

A female Black Leopard (*Felis pardus*) and a Leopard-Cat (*F. bengalensis*), from Thayetmyo, Burma, presented by Mr. J. A. P. Stuart.

3 Persian Gazelles (*Gazella subgutturosa*) and a Gmelin's Sheep (*Ovis orientalis*), from Persia, presented by Sir Percy Cox, K.C.M.G., Capt. R. E. Cheesman, C.M.Z.S., and Major Daly on June 6th.

3 American Bluebirds (*Sialia sialis*) and 2 Sacred Ibises (*Ibis æthiopica*), bred in the Menagerie.

4 Eastern Paradise Whydah-birds (*Steganura paradisea verreauxi*) and 4 East-African Colies (*Colius affinis*), both new to the Collection, presented by Mr. W. G. Keeping.

1 Greenland Falcon (*Hierofalco candicans*), captured at Boncath, Pembrokeshire, and presented by Col. Cecil Spence Colby, C.M.G., D.S.O.

A large collection of North-American reptiles and batrachians, including 10 Horrid Rattlesnakes (*Crotalus horridus*), 2 Copperheads (*Ancistrodon contortrix*), and 3 Mocassins (*Ancistrodon piscivorus*), presented by the New York Zoological Society.

A Striped Tree-Frog (*Megalixalus fornasinii*), new to the Collection, from Zanzibar, presented by Capt. W. H. Ingrams, F.Z.S.

JULY.

The registered additions to the Society's Menagerie during the month of July were 180 in number. Of these 112 were acquired by presentation, 20 were deposited, 1 was received in exchange, 21 were purchased, and 26 were born in the Menagerie.

The following may be specially mentioned:—

A collection of Mammals and Birds including 1 Serval (*Felis serval*), 2 Spotted Hyænas (*Hyæna crocuta*), 2 Harnessed Antelopes (*Tragelaphus scriptus*); 3 Collared Guinea-fowls (*Numida meleagris*), 2 Marabou Storks (*Leptoptilus crumeniferus*), 1 Ostrich (*Struthio camelus*), 1 Black-necked Crowned Crane (*Balearica pavonina*), from Gambia, presented by H.E. Capt. C. H. Armitage on July 19th.

1 Malayan Tapir (*Tapirus indicus*), born on July 14th.

2 Nylghaie (*Boselaphus tragocamelus*), born on July 5th.

2 Cape Hyrax (*Hyrax capensis*), born on July 31st.

1 Great Kangaroo (*Macropus giganteus*), 1 Red Kangaroo (*Macropus rufus*), purchased on July 6th.

1 Pygmy Flying Phalanger (*Acrobates pygmæa*), new to the Collection, deposited on July 6th; 1 Noisy Rat (*Rattus vociferans*), new to the Collection, from Kuala Lumpur, presented by C. Boden Kloss, Esq.

3 One-Streaked Hawks (*Asturinula monogrammica*) from the Northern Province of Nigeria, presented by J. R. C. Stephens on July 25th.

4 Ostriches (*Struthio camelus*) from an Ostrich Farm in Tunis, purchased on July 27th.

August.

The registered additions to the Society's Menagerie during the month of August were 231 in number. Of these 61 were acquired by presentation, 42 were deposited, 5 were received in exchange, 111 were purchased, and 12 were born in the Menagerie.

The following may be specially mentioned:—

A collection, principally from New Guinea and Aru, obtained by Mr. Frost, and comprising a few mammals and reptiles and about 100 birds, including four species of Birds-of-Paradise, some rare Doves and Parrots. The following species are new to our Collection:—3 Orange-fronted Fruit-Pigeons (*Ptilopus aurantiifrons*), 4 Stephani's Green-winged Pigeons (*Chalcophaps stephani*), 1 Lesser White Goshawk (*Astur leucosomus*), 3 Red-bellied Rails (*Eulabeornis castaneiventris*), 2 Brown-billed Brush-Turkeys (*Talegallus fuscirostris*), 1 Amboina King-Parrakeet (*Aprosmictus amboinensis*), 8 New Guinea Terrapins (*Emydura novæ-guineæ*), 1 Striped Gecko (*Gecko vittatus*): purchased on August 27th.

A collection of Mammals and Birds from Para, including 2 Red Brockets (*Mazama rufa*), 2 Crab-eating Raccoons (*Procyon cancrivorus*), 2 Maguari Storks (*Euxenura maguari*), 2 Cocoi Herons (*Ardea cocoi*), 2 Scarlet Ibises (*Eudocimus ruber*), and others: purchased on August 9th.

1 Lechee Antelope (*Cobus leche*), and 1 Wart-Hog (*Phacochœrus æthiopicus*), from S. Africa, deposited on August 31st.

1 Finch-billed Bulbul (*Spizixus canifrons*) and 1 White-winged Mynah (*Poliopsar nemoricola*), new to the Collection, from Yunnan, presented by J. D. La Touche, C.M.Z.S., on August 10th.

1 Nigerian Hare (*Lepus canopus*), new to the Collection, from Kano, N. Nigeria, deposited on August 11th.

September.

The registered additions to the Society's Menagerie during the month of September were 131 in number. Of these 56 were acquired by presentation, 20 were deposited, 14 were received in exchange, 37 were purchased, and 4 were born in the Menagerie.

The following may be specially mentioned:—

1 Abyssinian Oribi (*Ourebia montana*), from Kenya Colony, E. Africa, deposited on September 24th.

1 Broad-billed Roller (*Eurystomus crassirostris*), from the Aru Islands, new to the Collection, deposited on September 13th.

Mr. M. A. C. Hinton exhibited, and made remarks upon, an embryo African Elephant.

Mr. E. G. BOULENGER, F.Z.S., exhibited, and made remarks upon, photographs of a Common Grass Snake swallowing a Viper.

Mr. F. MARTIN DUNCAN, F.Z.S., exhibited a series of cinematograph films of Marine Animals, and asked the Society to accept the series for its Zoological Film Library.

Mr. D. SETH-SMITH, F.Z.S., exhibited a series of photographs of the Sacred Ibis nesting in the Society's Gardens, and said that the last occasion on which the birds had bred in the Gardens was in 1877, as recorded by the late Dr. P. L. Sclater in 'The Ibis' (1878, ser. 4, vol. ii. p. 449).

Prof. G. ELLIOT SMITH, F.R.S., F.Z.S., gave an account of the habits of *Tarsius*, and illustrated his remarks by a series of photographs of living specimens which had been taken by Mr. W. E. Le Gros Clark, F.Z.S., in Borneo.

November 8th, 1921.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,
in the Chair.

Mr. EDGAR P. CHANCE, M.A., M.B.O.U., gave an account of his investigation of the laying-habits of the Cuckoo (*Cuculus canorus*) and the life of the young Cuckoo, and illustrated his remarks with s striking series of cinematograph films and photographs.

November 22nd, 1921.

Prof. E. W. MACBRIDE, F.R.S., Vice-President,
in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of October, 1921:—

The registered additions to the Society's Menagerie during the month of October were 147 in number. Of these 48 were acquired by presentation, 36 were deposited, 10 were received in exchange, 34 were purchased, and 19 were born in the Menagerie.

The following may be specially mentioned:—

1 Bosman's Potto (*Perodicticus potto*), from Ilorin, Northern Provinces of Nigeria, presented by J. R. C. Stevens, Esq., on October 16th.

2 Maholi Galagos (*Galago maholi*), from Pretoria, received in exchange.

2 Snowy Owls (*Nyctea scandiaca*), from Northern Baffin's Land, presented by Henry Toke Munn, F.R.G.S., on October 8th.

1 Salvin's Razor-billed Curassow (*Mitua salvini*), from Ecuador, new to the Collection, deposited on October 11th.

2 Regal Horned Lizards (*Phrynosoma regale*), from Arizona, presented by E. Newitt on October 17th.

Mr. A. S. Le Souëf, C.M.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the early life-history of *Ornithorhynchus*.

Dr. A. Smith Woodward, F.R.S., V.P.Z.S., exhibited, and made remarks upon, a Human Skull and other remains from Broken Hill, North Rhodesia, upon which he had founded the species *Homo rhodesiensis*. In comparing the Rhodesian skull with a Neanderthal skull from La Chapelle, Dr. Smith Woodward stated that the former may prove to be the next grade after Neanderthal in the ascending series.

INDEX OF ILLUSTRATIONS.

Æpyprymnus rufescens, Fig. 77, p. 871.
Ailurus fulgens, Fig. 65, p. 589.
Alouatta caraya, Fig. 49, p. 516.
Amblonyx cinerea, Figs. 19, 21, pp. 536, 540.
Aonyx capensis, Figs. 19, 21, pp. 536, 540.
Aotus felinus, Fig. 46, p. 512.
Ateles ater, Fig. 42, p. 504.
—— *grisescens*, Figs. 37, 41, pp. 498, 503.
Aulonocara nyassæ, Pl. V., p. 675.

Bainia haughtoni, Fig. 38, p. 662.
—— *peavoti*, Fig. 37, p. 660.

Cacajao calva, Fig. 48, p. 514.
Callicebus moloch, Figs. 37, 45, pp. 498, 510.
Canis bengalensis, Fig. 64, p. 588.
Cebus albifrons, Fig. 40, p. 501.
—— *fatuellus*, Figs. 38, 39, pp. 499, 500.
Charronia flavigula, Figs. 27, 31, pp. 806, 815.
Chiromys, Fig. 68, p. 745.
Chlamydophorus, Fig. 12, p. 635.
Conepatus, Fig. 18, p. 483.
—— *proteus*, Figs. 29, 30, 37, 39, pp. 810, 812, 826, 829.
Cyrtocara annectens, Fig. 30, p. 723.

Dasyurus viverrinus, Fig. 77, p. 871.
Dendrolagus ursinus, Figs. 70, 74, 75, 77, 78, 79, pp. 855, 861, 862, 871, 873, 874.
Dicynodon andrewsi, Fig. 30, p. 651.
—— *curtus*, Fig. 33, p. 654.
—— *ictinops*, Fig. 35, p. 657.
—— *macrorhynchus*, Fig. 36, p. 658.
—— *osborni*, Fig. 31, p. 652.
—— *sollasi*, Figs. 28, 29, p. 649.
—— *watsoni*, Fig. 32, p. 653.
—— *woodwardi*, Fig. 34, p. 655.
Didelphys azaræ, Fig. 77, p. 871.
—— *marsupialis*, Fig. 77, p. 871.
Dinotherium giganteum, Figs. 1–4, pp. 527, 529, 530, 532.

Emydopsis longus, Fig. 41, p. 667.
—— *parvus*, Fig. 43, p. 670.
—— *sciuroides*, Fig. 42, p. 666.
—— *trigoniceps*, Fig. 42, p. 666.
Emyduranus platyops, Fig. 44, p. 671.
Endothiodon crassus, Fig. 45, p. 673.
Eosimops newtoni, Fig. 39, p. 663.

Galago crassicaudata, Fig. 69, p. 747.
Gale nivalis, Figs. 27, 30, 33, pp. 806, 812, 819.
Grison, Fig. 14, p. 475.
—— *furax*, Fig. 28, p. 808.
Grisonella sp., Figs. 18, 32, 39, pp. 483, 817, 829.
Gulo gulo, Figs. 14, 16, pp. 475, 479.

Hapale jacchus, Fig. 50, p. 518.
Haplochromis argyrosoma, Fig. 25, p. 714.
—— *atritæniatus*, Fig. 23, p. 711.
—— *auritus*, Fig. 14, p. 699.
—— *breviceps*, Fig, 9, p. 694.
—— *ericotænia*, Fig. 17, p. 704.
—— *eucinostomus*, Pl. IV., p. 675.
—— *fuscotæniatus*, Fig. 12, p. 697.
—— *lateristriga*, Fig. 18, p. 705.
—— *lepturus*, Fig. 22, p. 710,
—— *leuciscus*, Fig. 26, p. 715.
—— *longipes*, Pl. V., p. 675.
—— *macrochir*, Fig. 24, p. 713.
—— *macrorhynchus*, Fig. 28, p. 718.
—— *macrostoma*, Pl. IV., p. 675.
—— *melanonotus*, Fig. 21, p. 708.
—— *melanotænia*, Fig. 20, p. 707.
—— *micrentodon*, Fig. 27, p. 716.
—— *microstoma*, Fig. 10, p. 694.
—— *ornatus*, Fig. 6, p. 691.
—— *placodon*, Figs. 1, 5, pp. 685, 700.
—— *plagiotænia*, Fig. 19, p. 706.
—— *polystigma*, Pl. I., p. 675.
—— *præorbitalis*, Pl. III., p. 675.
—— *sexfasciatus*, Fig. 7, p. 692.
—— *similis*, Fig. 8, p. 693.
—— *simulans*, Fig. 5, p. 690.
—— *sphærodon*, Fig. 16, p. 704.
—— *spilorhynchus*, Pl. VI., p. 675.
—— *strigatus*, Fig. 13, p. 698.
—— *tetrastigmata*, Fig. 4, p. 685.
—— *urotænia*, Fig. 11, p. 696.
—— *woodi*, Pl. II., p. 675.
Helictis everetti, Figs. 14, 15, pp. 475, 477.
—— *personata*, Figs. 29, 35, 38, pp. 810, 823, 828.
Hemigalago demidoffi, Fig. 69, p. 747.
Hydrictis maculicollis, Figs. 19, 20, pp. 536, 538.

Ictonyx, Fig. 17, p. 481.
—— *capensis*, Figs. 29, 34, pp. 810, 821.

Lagothrix infumatus, Figs. 37, 43, 44, pp. 498, 506, 507.
Lamellipalpodes annandalei, Figs. 4, 5, p. 585.
Lamellipalpus bombayensis, Fig. 3, p. 582.
—— *nigripennis*, Figs. 1, 2, pp. 580, 581.
Lasiorhinus latifrons, Fig. 23, p. 597.
Lemur catta, Figs. 66–69, pp. 743–745, 747.
—— *fulvus*, Figs. 68, 69, pp. 745, 747.
—— —— *rufifrons*, Figs. 66, 67, 69, pp. 743, 744, 747.
—— *macaco*, Figs. 67–69, pp. 743–745, 747.
—— *mongoz*, Figs. 67, 68, pp. 744, 745.
—— *rubriventer*, Fig. 67, p. 744.
Leontocebus, Fig. 51, p. 520.
Lethrinops leptodon, Fig. 29, p. 721.
Liponyssus æthiopicus, Fig. 27, p. 785.
—— *biscutatus*, Figs. 21, 22, pp. 778, 779.
—— *blanchardi*, Figs. 28, 30, 31, pp. 785, 787, 788.
—— *ellipticus*, Fig. 36, p. 795.
—— *flavus*, Figs. 34, 35, pp. 792, 793.
—— *granulosus*, Fig. 35, p. 793.
—— *longimanus*, Fig. 37, p. 796.
—— *macedonicus*, Figs. 32, 33, pp. 790, 791.
—— *madagascariensis*, Figs. 23, 24, pp. 780, 781.
—— *sciurinus*, Figs. 28, 29, pp. 785, 786.
—— *sternalis*, Figs. 25, 26, pp. 782, 783.
—— *viator*, Fig. 20, p. 776.
Loris gracilis, Fig. 69, p. 747.
Lutra lutra, Figs. 15, 19, 20, pp. 477, 536, 538.
Lyncodon patagonicus, Figs. 30, 35, pp. 812, 823.

Macropus bennetti, Figs. 70, 77, pp. 855, 871.
—— *giganteus*, Fig. 71, p. 858.
Marmosa elegans, Fig. 77, p. 871.
Martes foina, Figs. 16, 27, pp. 479, 806.
—— *martes*, Fig. 16, p. 479.

Megalohyrax pygmæus, Fig. 1, p. 843.
Meles meles, Figs. 14, 16, 65, pp. 475, 479, 589.
Mellivora ratel, Figs. 14, 17, pp. 475, 481.
Mephitis sp., Figs. 14, 18, pp. 475, 483.
—— *mephitica*, Figs. 29, 36, pp. 810, 824.
Metachirus opossum, Figs. 75, 76, 77, pp. 862, 864, 871.
Mydaus meliceps, Figs. 29, 37, pp. 810, 826.
Mystax ursulus, Fig. 52, p. 522.

Neonyssus intermedius, Figs. 18, 19, p. 772.
Nestling feathers, Figs. 1–14, pp. 612, 614, 616, 619, 620, 622, 624, 629, 637, 638; Pls. I.–X., p. 609.
Nycticebus tardigradus, Fig. 69, p. 747.

Onychogale lunata, Fig. 70, p. 855.
Otopharynx selenurus, Fig. 1, p. 679.

Palemydops platysoma, Fig. 40, p. 665.
Paratetranychus trinitatis, Figs. 42, 43, pp. 801, 802.
Perameles obesula, Figs. 72, 75, 76, 77, pp. 859, 862, 864, 871.
Perodicticus potto, Fig. 69, p. 747.
Petaurus breviceps, Figs. 75, 77, pp. 862, 871.
—— *papuanus*, Fig. 77, p. 871.
—— *sciureus*, Figs. 73, 75, 77, pp. 860, 862, 871.
Phalanger maculatus, Figs. 22, 24, pp. 595, 600.
—— *orientalis*, Fig. 77, p. 871.
Philander laniger, Fig. 77, p. 871.
Pithecia satanas, Fig. 47, p. 513.
Phascolarctos cinereus, Figs. 23, 25, 26, 53, 54, 56, 58–63, pp. 548, 549, 551, 556, 558, 561, 566, 573, 574, 597, 603, 605; Pls. V., VI., p. 547.
Phascolomys ursinus, Figs. 23, 25, 26, pp. 597, 603, 605.
Plesiogale nudipes, Fig. 33, p. 819.
Podapolipus aharonii, Fig. 41, p. 800.
Pœcilictis, Fig. 17, p. 481.
Pœcilogale albinucha, Figs. 30, 32, pp. 812, 817.
Pseudochirus peregrinus, Pl. V., p. 577; Figs. 22, 24, pp. 595, 600.
Pseudotropheus tropheops, Figs. 2, 3, pp. 681, 684.
Putorius putorius, Figs. 15, 27, 33, pp. 477, 806, 819.

Rana temporaria, Fig. 1, p. 494.
Rhamphochromis macrophthalmus, Pl. VI., p. 675.
Rhinonyssoides trouessarti, Fig. 17, p. 770.
Rhinonyssus novæ-guineæ, Fig. 16, p. 769.

Sagartia luciæ, Figs. 1–4, pp. 730, 731, 735, 736.
Sarcophilus harrisi, Figs. 70, 77, pp. 855, 871.
Spilogale putorius, Figs. 29, 36, pp. 810, 824.

Tarsius spectrum, Fig. 69, p. 747.
Tarsonemus translucens, Figs. 38–40, pp. 798, 799.
Taxidea, Fig. 18, p. 483.
Tayra barbara, Figs. 16, 28, 31, 38, pp. 479, 808, 815, 828.
Titanohyrax andrewsi, Fig. 6, p. 848.
—— *ultimus*, Figs. 2–5, pp. 845–847.
Trichosurus vulpecula, Figs. 22, 24, 26, 55, 57, 58, 61, pp. 550, 552, 556, 566, 595, 600, 605; Pl. V., p. 547.
Tropheus moorii, Fig. 2, p. 681.

Varanus bengalensis, Figs. 1–4, pp. 488, 490–492.

Zoogeographical Map Caucasus and Western Asia, Fig. 1, p. 454.

INDEX.

1921.—Pages 447–887.

[New names in clarendon type. Systematic references in italics.
(z. s. l.) indicates additions to the Society's Menagerie.]

Acrida nasuta, 459.
—— *robusta*, 458.
—— *turrita turrita*, 464, 469.
Acrobates pygmæa (z. s. l.), 884.
Acrotylus longipes, 457.
Actinia chrysosplenium, 734, 737, 738.
—— *pallida*, 738.
Æpyprymnus, 854, 878.
—— *rufescens*, 854, 855, 857, 872, 874.
Aiptasia (Heteractis) lucida, 737.
Ailurus, 473, 474.
—— *fulgens*, 587, 589.
Alouatta (=*Mycetes*), 515.
—— *caraya*, 515.
Amblonyx, 543, 544, 811, 814, 830.
Ameles abjecta, 451.
Amphisbæna alba (z. s. l.), 883.
Anas boscas, 609.
Ancistrodon contortrix (z. s. l.), 884.
—— *piscivorus* (z. s. l.), 884.
Anterastes serbicus, 457.
Anthropopithecus troglodytes, 757, 758, 761.
Aonyx capensis, 535, 537, 541, 542, 543, 544, 803, 830.
Aotus, 511.
—— *felinus*, 511.
Aprosmictus amboinensis (z. s. l.), 885.
Arctonyx, 473, 474, 803, 805, 828, 833.
Arcyptera flavicosta transcaucasia, 463, 467, 471.
—— —— *flavicosta*, 469.
—— *fusca*, 458, 470.
Ardea cocoi (z. s. l.), 885.
Astatotilapia, 680.
—— *calliptera*, 680.
Astur leucosomus (z. s. l.), 885.
Asturinula monogrammica (z. s. l.), 884.
Ateles, 502.
—— *ater*, 503.
—— *grisescens*, 502, 757.
—— *melanochir*, 505.
—— *paniscus*, 505.
Aulonocara, gen. n., 726.
—— **nyassæ**, sp. n., 727.
Axis porcinus (z. s. l.), 883.

Bainia, gen. n., 659.
—— **haughtoni**, sp. n., 661.
—— **peavoti**, sp. n., 659.
—— **tigriceps** (Owen), sp. n., 659.
Balearica pavonina (z. s. l.), 884.
Bettongia penicillata, 851, 865.
Blepharis mendica, 467.
Bos caffer (z. s. l.), 883.
Boselaphus tragocamelus (z. s. l.), 88.

Bradypus tridactylus, 564, 872.
Brunnerella mirabilis, 465, 466.
Bunohyrax, 841.

Cacajao, 514.
—— *calva*, 514.
Callicebus, 509.
—— *brunnea*, 511.
—— *moloch*, 509.
—— *personata*, 501.
Callimenus dilatatus, 451.
Canis bengalensis, 587.
—— *thous* (Z. S. L.), 883.
Cebidæ, 497, 759.
Cebus albifrons, 500.
—— *apella*, 502.
—— *capucinus*, 501.
—— *fatuellus*, 498, 758, 762.
—— *hypoleucos*, 501.
Celes variabilis carbonaria, 463, 467, 471.
—— —— *variabilis*, 469.
Cercopithecidæ, 759.
Cercopithecus æthiops, 761.
—— *patas*, 757.
—— *preussi*, 762.
—— *tantalus*, 757.
Cervus eldi (Z. S. L.), 883.
Chalcophaps stephani (Z. S. L.), 885.
Charora crassivenosa, 466.
Charronia, 474, 476, 485, 539, 807, 811, 814, 816, 817, 832.
—— *flavigula*, 478.
Chilotilapia, 679.
—— *rhoadesii*, 680.
Chiromyidæ, 759.
Chiromys madagascariensis, 751, 758, 760.
Chironectes, 855.
Chlamydophorus, 634.
Chrysochraon brachypterus, 470.
—— *dispar*, 448, 469, 470.
Chrysoela chrysosplenium, 738.
Cobus leche (Z. S. L.), 885.
Cænolestes obscurus, 851–882.
Colius affinis (Z. S. L.), 884.
Conepatus, 474, 476, 485, 803, 811, 813, 814, 825, 827, 829, 837.
Conepatus proteus, 484, 809, 825.
Corematodus, 677.
—— *shiranus*, 677.
Crotalus horridus (Z. S. L.), 884.
Cuculligera maculinervis, 459.
Cuculus canorus, 886.
Cuscus maculatus, 866.
Cynælurus jubatus (Z. S. L.), 883.
Cynotilapia afra, 684.
Cyrtocara, 722.
—— **annectens**, sp. n., 723.
—— *moorii*, 724.
—— *venusta*, 722.

Dasyuridæ, 851, 858, 869, 877.
Dasyurus macrurus, 866.
—— *viverrinus*, 851, 854, 857, 866, 871, 874, 877.
Decticus verrucivorus schugurovi, 469.
—— —— *verrucivorus*, 455, 470, 471.
Dendrolagus, 853, 854, 857, 859, 869, 880.
—— *bennetti*, 851, 862, 863, 867, 869.
—— *dorianus*, 852, 853, 860, 869.
—— *inustus*, 863, 869.
—— *ursinus*, 851–882.
Derocorys roseipennis lazurescens, 465, 467.
—— —— *roseipennis*, 467.
Dicynodon andrewsi, sp. n., 650.
—— **curtus**, sp. n., 654.
—— **ictinops**, sp. n., 656.
—— **macrorhynchus**, sp. n., 657.
—— **osborni**, sp. n., 651.
—— **sollasi**, sp. n., 648.
—— **watsoni**, sp. n., 653.
—— **woodwardi**, sp. n., 655,
Didelphyidæ, 851, 854, 858, 877.
Didelphys, 851, 852, 856, 861, 870, 877.
—— *albiventris*, 851.
—— *azaræ*, 851, 852, 854, 857, 870, 874.
—— *marsupialis*, 851, 854, 857, 870, 874.
—— *virginiana*, 863, 868.
Dinotherium giganteum, 525.
—— *naui*, 526.

Diprotodon, 606.
Diprotodontia, 858, 868, 878.
Docimodus, 721.
—— *johnstoni*, 722.
Dolichopoda euxina, 459.
Dorcopsis luctuosa, 857.
Drymadusa curvicercis, 459.
—— *grisea*, 465, 466.
—— *konowi*, 459, 466.
—— *recticauda*, 459.
—— *spectabilis*, 459.
Duronia, 452.
—— *fracta fracta*, 467.
—— —— *kalmyka*, 467.

Empusa pennicornis, 459, 462.
Emydops parvus, sp. n., 669.
Emydopsis, gen. n., 666.
—— **longus**, sp. n., 667.
—— **sciuroides**, sp. n., 668.
—— **trigoniceps**, sp. n., 666.
Emydura novæ-guineæ (z. s. l.), 885.
Emyduranus platyops, gen. et sp. n., 670.
Endothiodon crassus, sp. n., 672.
Enhydris, 473.
Eosimops newtoni, gen. et sp. n., 663.
Epacromia tergestina, 469.
Eremiaphila genei, 458.
—— *persica*, 464, 467.
Eudocimus ruber (z. s. l.), 885.
Eulabeornis castaneiventris (z. s. l.), 885.
Eurystomus crassirostris (z. s. l.), 885.
Euxenura maguari (z. s. l.), 885.

Felis bengalensis (z. s. l.), 884.
—— *leo* (z. s. l.), 644, 883.
—— *pardus* (z. s. l.), 884.
—— *serval* (z. s. l.), 884.
—— *tigris* (z. s. l.), 883.
Fischeria baltica, 467.
—— *bætica*, 451.

Galagidæ, 759.
Galago, 763.
—— *crassicaudata*, 750.
Galago maholi (z. s. l.), 887.
Gale, 807, 811–814, 818, 832.
—— *africana*, 817.
—— *nivalis*, 807, 817.
Galera, 473, 476, 803.
—— *barbara* (z .s. l.), 883.
Gampsocleis recticauda, 457.
—— *schelkovnikovæ*, 455.
Gazella subgutturosa (z. s. l.), 884.
Gecko vittatus (z. s. l.), 885.
Gelastorrhinus, 452.
—— *sagitta*, 467.
Geniohyus, 841, 850.
Geomantis larvoides, 457.
Gomphocerus caucasicus, 458.
—— *maculatus*, 467.
—— *sibiricus*, 448, 458, 470.
—— *variegatus*, 453.
Gorilla gorilla, 757, 758, 760, 765.
—— —— *beringeri*, 643.
—— —— *matschiei*, 643.
Gratidia bituberculata, 465.
Grison, 473, 474, 476, 803, 807, 811, 820, 827, 835.
—— *furax*, 807, 813–816.
Grisonella, 480, 482, 484, 485, 807, 813, 814, 816, 829, 835.
Grisoninæ, subfam. n., 835.
Gryllodes odicus, 469.
Gryllus domesticus, 448.
—— *frontalis*, 458.
—— *hebræus*, 458.
—— *lateralis*, 451, 462.
—— *tartarus obscurus*, 458.
—— (*Gryllodes*) *kerkennensis*, 451.
Gulo, 473, 474, 476, 478, 480, 485, 803, 805, 811, 813, 814, 820, 822, 827, 828, 833.
—— *gulo*, 478, 539.
Guloninæ, 833.
Gymnopus, 818.
Gypagus papa (z. s. l.), 644.

Hapale, 517.
—— *jacchus*, 517, 758.
—— *penicillata*, 519.
—— *pygmæa*, 519.
Hapalemur, 763, 766, 767.

Hapalidæ, 517, 759, 766, 767.
Haplochromis, 685.
—— **argyrosoma**, sp. n., 713.
—— **atritæniatus**, sp. n., 711.
—— **auritus**, sp. n., 699.
—— **breviceps**, sp. n., 694.
—— *brevis*, 709.
—— *cæruleus*, 712.
—— *chrysonotus*, 702.
—— *compressiceps*, 717.
—— *dimidiatus*, 698.
—— **ericotænia**, sp. n., 704.
—— **eucinostomus**, sp. n., 716.
—— **fuscotæniatus**, sp. n., 696.
—— **guentheri**, sp. n., 707.
—— **holotænia**, sp. n., 697.
—— *intermedius*, 701.
—— *johnstoni*, 691.
—— *kirkii*, 693.
—— *lateristriga*, 705.
—— **lepturus**, sp. n., 709.
—— **leuciscus**, sp. n., 714.
—— *livingstonii*, 688.
—— **longipes**, sp. n., 712.
—— **macrochir**, sp. n., 712.
—— *macrophthalmus*, 714.
—— **macrorhynchus**, sp. n., 717.
—— **macrostoma**, sp. n., 719.
—— **maculimanus**, sp. n., 689.
—— **melanonotus**, sp. n., 708.
—— **melanotænia**, sp. n., 706.
—— **micrentodon**, sp. n., 715.
—— **microstoma**, sp. n., 695.
—— *modestus*, 701.
—— *nototænia*, 709.
—— **ornatus**, sp. n., 691.
—— **placodon**, sp. n., 700.
—— **plagiotænia**, sp. n., 706.
—— **polystigma**, sp. n., 688.
—— **præorbitalis**, sp. n., 717.
—— **quadrimaculatus**, sp. n., 703.
—— *rhoadesii*, 710.
—— *rostratus*, 718.
—— **sexfasciatus**, sp. n., 692.
—— **similis**, sp. n., 693.
—— **simulans**, sp. n., 689.
—— **sphærodon**, sp. n., 703.
—— **spilorhynchus**, sp. n., 711.
Haplochromis **strigatus**, sp. n., 697.
—— *subocularis*, 690.
—— *tetrastigma*, 699.
—— **urotænia**, sp. n., 695.
—— **woodi**, sp. n., 702.
Helictidinæ, 831.
Helictis, 473, 474, 476, 484, 803, 831.
—— *everettii*, 480.
Heliopteryx humeralis, 459, 466.
Helioscirtus moseri moseri, 467.
—— —— *tichomirovi*, 465, 467.
Hemigalago demidoffi, 750.
Hemitilapia, 677.
—— *oxyrhynchus*, 677.
Hierodula, 452.
Hierofalco candicans (z. s. l.), 884.
Homo, 757, 760, 761.
—— **rhodesiensis**, sp. n., 887.
Hyæna crocuta (z. s. l.), 884.
Hyalorrhipis clausi, 469.
Hydrictis, 544, 813, 830.
Hylobates lar, 757.
Hypsiprymnodon, 607.
Hyrax capensis (z. s. l.), 884.

Ibis æthiopica (z. s. l.), 884.
Ictonychinæ, 835.
Ictonyx, 474, 476, 482, 485.
—— (*Zorilla*), 803, 807, 811, 813, 814, 820-822, 828, 835.
Indris brevicaudatus, 746.
Isophya adelungi, 462, 463, 467.
—— *acuminata*, 459, 462.
—— *amplipennis*, 462.
—— *bivittata*, 463.
—— *paveli*, 457.
—— *poltoratskyi*, 459.
—— *pyrenæa*, 462, 463.
—— *rodsjankoi*, 459.
—— *schmidti*, 467.

Jaculus jaculus, 645.
—— *jaculus* (z. s. l.), 883.
—— *orientalis*, 645.
—— *orientalis* (z. s. l.), 883.

Kolonakus, 832.
Kurdia nesterovi, 459.

Lagothrix, 506.
—— *humboldtii*, 509.
—— *infumatus*, 506.
Lamellipalpodes, gen. n., 579, 584.
—— **annandalei**, sp. n., 584.
Lamellipalpus, gen. n., 579.
—— *nigripennis*, 580.
Lasiorhinus latifrons, 598.
Latax, 831.
Lataxinæ, nom. nov., 830.
Lemur, 742, 758, 766.
—— *catta*, 743, 758.
—— *fulvus*, 743.
—— —— *rufifrons*, 743.
—— *macaco*, 743.
—— *melanocephala*, 743.
—— *mongoz*, 743.
—— *rubriventer*, 743.
—— *varius*, 743.
Lemuridæ, 742, 759.
Leontocebus, 520.
—— *rosalia*, 520.
Lepidosiren, 495.
Leptophyes albovittata, 467.
—— *punctatissima*, 448, 453.
Leptoptilus crumeniferus (z. s. l.), 884.
Leptoternis gracilis, 467.
Lepus canopus (z. s. l.), 885.
Lethrinops, gen. n., 719.
—— **albus**, sp. n., 719.
—— **leptodon**, sp. n., 721.
—— *lethrinus*, 720.
—— **macrorhynchus**, sp. n., 720.
Limnodynastes peronii, 493.
Liogryllus bimaculatus, 452.
Liponyssus, 773.
—— **æthiopicus**, sp. n., 774, 783.
—— *arcuatus*, 774.
—— *bacoti*, 775.
—— **biscutatus**, sp. n., 774, 779.
—— *blanchardi*, 774, 787.
—— *bursa*, 775.
—— *carnifex*, 774.
—— **chiropteralis**, nom. nov., 773, 776.
—— **confucianus**, nom. nov., 774, 789.
Liponyssus creightoni, 774.
—— *ellipticus*, 774, 795.
—— *flavus*, 774, 791.
—— *granulosus*, 774, 794.
—— *javensis*, 774.
—— *lacertinus*, 775.
—— *liberiensis*, 774.
—— *longimanus*, 796.
—— **macedonicus**, sp. n., 774, 789.
—— **madagascariensis**, sp. n., 774, 780.
—— *natricis*, 773, 775.
—— **nyassæ**, sp. n., 773, 777.
—— *saurarum*, 775.
—— **sciurinus**, sp. n., 774, 785.
—— *serpentium*, 773.
—— *silviarum*, 775.
—— **sternalis**, sp. n., 774, 781.
—— **viator**, sp. n., 773, 775.
Locusta caudata caudata, 455, 470.
—— —— *kolenatii*, 458.
Loris gracilis, 748.
Lorisidæ, 747, 759.
Lutra, 473, 476, 478, 484, 544, 803, 811, 813, 827, 828, 830.
—— *barang*, 479.
—— *cinerea*, 479, 535, 537, 539, 541.
—— *lutra*, 474, 535, 537, 539, 541.
—— *maculicollis*, 479, 535, 537, 541.
Lutreola, 818, 832.
Lutrinæ, 830.
Lyncodon, 474, 482, 539, 804, 814, 822, 827, 836.
Lyncodontinæ, subfam. n., 836.

Macacus leoninus (z. s. l.), 883.*
Macropodidæ, 851, 853, 854, 871, 878.
Macropus, 851, 853, 854, 857, 865, 869, 878.
—— *bennetti*, 851, 856, 865, 866, 867, 872, 874.
—— *giganteus*, 851–882.
—— *giganteus* (z. s. l.), 884.
—— *melanops*, 851.
—— *rufus*, 851, 852, 853, 868.
—— *rufus* (z. s. l.), 884.
Marmosa, 851, 877.

Marmosa elegans, 851, 854, 857, 867, 870, 877.
Martes, 473, 474, 476, 803, 805, 809, 811–814, 816, 817, 820, 822, 827, 832.
—— *foina*, 478, 480, 485, 816.
—— *martes*, 478, 480, 485, 816.
Martinæ, 832.
Mazama rufa (Z. S. L.), 885.
Meconema thalassinum, 448, 471.
Mecostethus grossus, 448, 470.
Medecticus assimilis, 458.
Megalixalus fornasinii (Z. S. L.), 884.
Megalohyrax, 839, 841, 844.
—— *eocænus*, 840, 841.
—— *minor*, 840, 842.
—— *niloticus*, 840, 843.
—— *palæotherioides*, 844.
—— **pygmæus**, sp. n., 840, 843.
—— *suillus*, 840, 843.
Meles, 473, 474, 476, 478, 480, 481, 482, 485, 803, 805, 809, 811, 813, 814, 822–829, 833.
—— *meles*, 478, 587, 590.
Melinæ, 803, 833.
Mellivora, 473, 474, 476, 481, 482, 485, 803, 805, 809, 814, 825, 827, 828, 835.
Mellivorinæ, 834.
Melogale, 811, 813, 814, 823, 824, 831.
—— *personata*, 805, 809, 811, 822.
Melursus ursinus (Z. S. L.), 644.
Mephitinæ, 836.
Mephitis, 473, 474, 476, 480, 484, 485, 803, 809, 811, 813, 814, 825, 827, 829, 837.
Metachirus, 851, 853, 877.
—— *opossum*, 851–882.
Metridium, 730.
—— *senilis*, 737.
Microcebus murinus, 746, 766.
Mitua salvini (Z. S. L.), 887.
Mixohyrax, 839, 841, 843.
Mœritherium, 532, 533.
Muntiacus muntjack (Z. S. L.), 883.
Mustela, 473, 474, 476, 484, 893, 807, 812, 814, 816, 821, 822, 827, 828, 832.
Mustela africana, 480.
—— *erminea*, 480.
—— *hibernica*, 480.
—— *nivalis*, 480.
Mustelidæ, 473, 803.
Mustelinæ, 803, 832
Mydainæ, 834.
Mydaus, 473, 474, 484, 803, 809, 811, 814, 826, 834.
Myrmecophila ochracea, 455.
Mystax, 521.
—— *mystax*, 522.
—— *ursulus*, 521, 758.

Nemobius heydeni, 462.
—— *tartarus*, 455, 463.
Neogale, 820.
Neonyssus, gen. n., 771.
—— **intermedius**, sp. n., 771.
Nocarodes rimansonæ, 463.
—— *schelkovnikovi*, 465.
—— *serricollis*, 451, 455, 459.
—— *woronowi*, 465.
Numida meleagris (Z. S. L.), 884.
Nyctea scandiaca (Z. S. L.), 887.
Nycticebus tardigradus, 747.

Octodon, 852.
Œdaleus mlokosiewitchi, 458.
Œdipoda caucasica, 469.
—— *schochi*, 451.
—— —— *schochi*, 459.
Œdipomidas, 523.
Œdipus, 523.
Olynthoscelis annulipes, 459.
—— *chabrieri*, 457.
—— *distincta*, 463.
—— *fallax*, 463.
—— *grisea*, 458.
—— *griseoaptera*, 470.
—— *indistincta*, 459, 467.
—— *kurda*, 459.
—— *prasina*, 457.
—— *punctifrons*, 461.
—— *satunini*, 452, 465, 466.
—— *signata*, 457, 459.
—— *zebra*, 459.

Onychogale lunata, 851, 856, 857, 863, 869.
Ornithorhynchus, 887.
Orphania scutata zacharovi, 455.
Otopharynx, 678.
—— *auromarginatus*, 678.
—— **selenurus**, sp. n., 679.
Ourebia montana (z. s. l.), 885
Otis orientalis (z. s. l.), 881.
Oxythespis wagneri, 467.

Palæomastodon, 533.
Palamydops platysoma, gen. et sp. n., 665.
Pallasiella bolivari, 466.
—— *truchmana*, 458.
Pamphagus brunnerianus, 459.
—— *yersini*, 459.
Papio, 762.
Paracaloptenus caloptenoides, 457.
Paradrymadusa beckeri, 455.
—— *borquilloni*, 452, 465.
—— *longipes*, 465.
—— *pastuchovi*, 452, 465.
—— *persa*, 452, 465.
—— *satunini*, 465.
—— *sordida*, 451, 459, 462, 467.
Paraonyx, 544, 811.
Parapleurus alliaceus, 458, 464, 470.
Paratetranychus, 801.
—— **trinitatis**, sp. n., 801.
Paratettix meridionalis, 462.
Peragale lagotis, 855, 864.
Perameles, 853, 856, 877.
—— *lagotis*, 871.
—— *nasuta*, 870.
—— *obesula*, 851–882.
Peramelidæ, 851, 854, 855, 869, 877.
Perodicticus potto (z. s. l.), 887.
—— *potto*, 749, 758.
Petaurus australis, 851, 866.
—— *breviceps*, 851, 862, 865, 866, 869, 872.
—— —— *papuanus*, 851, 154, 857, 865, 869, 872.
—— *sciureus*, 851–874.
Petrogale penicillata, 852.
—— *xanthopus*, 852, 853.
Pezotettix giornai, 453.
—— *rugulosa*, 459.
Phacochœrus æthiopicus (z. s. l.), 885.
Phalanger, 594, 596, 599, 601, 604, 606, 879.
—— *maculatus*, 598.
—— *orientalis*, 851, 856, 857, 869, 872.
Phalangeridæ, 851, 853, 878.
Phascogale, 866.
Phascolarctidæ, 879.
Phascolarctos, 591, 594, 596, 598, 599, 601, 602, 694–606, 879.
—— *cinereus*, 547, 553, 559, 560, 563, 565, 567–569, 572, 852–880.
Phascolomys, 596, 598, 599, 601, 602, 604, 606, 854, 855, 870.
—— *mitchelli*, 565, 866, 870.
—— *ursinus*, 594, 596.
Philander, 851, 877.
—— *laniger*, 851, 852, 854, 857, 870, 874.
Phonochorion satunini, 459.
Phrynosoma regale (z. s. l.), 887.
Pithecia, 512.
—— *monachus*, 514.
—— *satanas*, 512, 762.
Platycleis bicolor, 471.
—— *burri*, 467.
—— *capitata*, 464.
—— *daghestanica*, 445.
—— *decticiformis*, 457.
—— *escalerai*, 458.
—— *fusca*, 455.
—— *grisea*, 467.
—— *iljenskii*, 471.
—— *montana*, 469.
—— *nigrosignata*, 457.
—— *persica*, 452, 465, 466.
—— *roeseli*, 470.
—— *schereri*, 457.
—— *squamiptera*, 459, 466.
—— *truncata*, 457.
—— *vittata*, 463, 467.
—— *weseli*, 471.
Platypterna tibialis, 467.
Plesiogale, 805, 812–814, 820, 832.
—— *nudipes*, 805, 813.

Plesiogale strigidorsa, 818.
Podapolipus, 800.
—— **aharonii**, sp. n., 800.
Podisma koenigi. 463.
—— *pedestris*, 448, 470.
Pœcilictis, 473, 474, 476, 482, 485, 813, 814, 820, 821, 835.
Pœcilimon bosphoricus, 462, 467.
—— *concinnus*, 459.
—— *distinctus*, 462, 463, 467.
—— *kutahiensis*, 459.
—— *similis*, 455.
—— *syriacus*, 459.
—— *tschorochensis*, 459.
Pœcilimonella derjugini. 459.
Pœcilogale, 474, 480, 813, 814, 820.
Poliopsar nemoricola (z. s. l.). 885.
Polyprotodontia, 857, 877.
Potos caudivolvulus (z. s. l.), 883.
Presbytes, 762.
Procyon cancrivorus (z. s. l.), 885.
Protopterus, 495.
Pseudochirus, 594, 599, 601. 602, 604, 606, 854, 870.
—— *peregrinus*. 554, 557, 596, 851, 857, 868, 872, 874.
Pseudotropheus, gen. n., 681.
—— *auratus*, 693.
—— **novemfasciatus**, sp. n., 683.
—— **tropheops**, sp. n., 683.
—— *williamsi*, 682.
—— *zebra*, 682.
Psophus stridulus, 448, 453, 470.
Ptilopus aurantiifrons (z. s. l.), 885.
Putorius, 480, 484, 803, 807, 811, 812 814, 827, 832.
—— *furo*, 480, 817.
—— *nigripes*, 817.
—— *putorius*, 480, 817.
Pyrgodera armata, 458, 466.
Pyrgomorpha, 452.

Rana temporaria, 493.
Rattus vociferans (z. s. l.). 884.
Rhabdogale [= *Ictonyx*], 473.
Rhamphochromis, gen. n., 724.
—— *esox*, 726.
—— **ferox**, sp. n., 725.
Rhamphochromis leptosoma, sp. n., 726.
—— *longiceps*, 724.
—— **macrophthalmus**, sp. n., 725.
—— **woodi**, sp. n., 725.
Rhinoceros sondaicus, 643.
Rhinonyssoides, gen. n., 770.
—— **trouessarti**, sp. n., 770.
Rhinonyssus novæ-guineæ, sp. n., 769.

Saga cappadocica, 459.
Sagartia luciæ. 729.
—— *pustulata*, 733.
Saghatherium, 843.
Saimiris, 509.
—— *sciurea*, 509.
Sarcophilus, 605, 854, 856, 877.
—— *harrisi*, 851, 852, 854, 857. 859, 874.
Saxa pedo. 469.
Scarturus tetradactylus, 645.
—— *tetradactylus* (z. s. l.), 883.
Schistocerca peregrina, 467.
Scintharista brunneri, 465, 467.
Selenidera maculirostris (z. s. l.), 644.
Serranochromis, 685.
—— *thumbergii*, 685.
Sialia sialis (z. s. l.), 884.
Simia satyrus, 758, 759, 761, 765, 766.
Simiidæ, 759.
Sphingonotus balteatus, 458.
Sphodromerus, 452.
—— *cœlosyriensis*, 459.
—— *serapis*, 467.
Spilogale, 474, 476, 485, 803, 809, 811, 813, 814, 815, 837.
Spizixus canifrons (z. s. l.). 885.
Stauronotus anatolicus, 458.
—— *brevicollis*, 457, 469.
—— *hauensteini*, 451.
—— *kraussi*, 469.
—— *kurda*, 459.
Steganura paradisea verreauxi (z. s. l.), 884.
Stenobothrus apricarius, 458, 470.

Stenobothrus fischeri, 458.
—— *hæmorrhoidalis*, 458, 469, 470.
—— *lineatus*, 463.
—— *macrocerus*, 458, 464.
—— *nigromaculatus*, 453, 458, 470.
—— *parallelus*, 467.
—— *petræus*, 467.
—— *pulvinatus*, 458.
—— *scalaris*, 453, 458, 470.
—— *simplex*, 458.
—— *ventralis*, 453, 470.
—— *viridulus*, 448, 470.
—— *werneri sviridenkoi*, 471.
Strix flammea, 635.
Struthio camelus (z. s. l.), 884.
Symphalangus syndactylus, 759.

Talegallus fuscirostris (z. s. l.), 885.
Tamandua tetradactyla, 856, 874.
Tapirus indicus (z. s. l.), 884.
Tarsiidæ, 759.
Tarsipes, 607.
Tarsius, 886.
—— *spectrum*, 753, 758, 760, 767.
Tarsonemidæ, 797.
Tarsonemus translucens, 797.
Taxidea, 473, 474, 476, 482, 485, 803, 805, 807, 811, 813, 814, 821, 825, 827, 829, 835.
Taxidiinæ, 835.
Tayra (=*Galera*), 476, 480, 485, 803, 811, 813, 814, 715, 416, 827, 833.
—— *barbara*, 478, 807, 811.
Tayrinæ, subfam. n., 833.
Testudo ibera, 645.
—— *leithii*, 615.
Tetrabelodon angustidens, 633.
Tetranychidæ, 891.
Tettix bipunctata, 470.
—— *depressa*, 462.
—— *subulata*, 470.
Thalpomena ledereri, 459, 462.
—— *persa*, 465.
Thylacinus, 605, 866.
Tilapia, 676.
—— *melanopleura*, 677.
—— *mossambica*, 677.
—— *shirana*, 677.
—— *squamipinnis*, 677.
Titanohyrax, gen. n., 839, 841 844.
—— **andrewsi**, sp. n., 845, 847.
—— *palæotherioides*, 845, 847.
—— **schlosseri**, nom. n., 844, 847.
—— **ultimus**, sp. n., 844, 845.
Tmethis bilobus, 459.
—— *carinatus*, 459, 465.
—— *cisti*, 459.
—— *escherichi*, 459.
—— *holtzi*, 459.
—— *persa*, 465.
—— *muricatus*, 499.
—— *zaitzevi*, 463.
Tragelaphus scriptus (z. s. l.), 884.
Trichosurus, 596, 602, 694–606, 854, 866, 879.
—— *vulpecula*, 547, 549, 553, 554, 557, 559, 563, 564, 567, 569, 852–880.
Tridactylus tartarus, 469.
Trinchus schrenki, 466.
Troglophilus escalerai, 459.
Tropidauchen, 452.
Tropidopola cylindrica, 452.

Urticina felina, 737.

Varanus arenarius, 487.
—— *bengalensis*, 487.
—— *exanthematicus*, 487.
—— *griseus*, 487.
—— *niloticus*, 417.
Vormela, 474, 484, 803, 832.

Zorilla [=*Ictonyx*], 803.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

No. 217.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

May 10th, 1921.

Dr. A. Smith Woodward, LL.D., F.R.S., Vice-President, in the Chair.

Sir S. F. Harmer, K.B.E., F.R.S., exhibited, and made remarks upon, a mounted specimen of *Rhinoceros sondaicus*.

Mr. Thos. Gerrard, F.Z.S., exhibited, and made remarks upon, a series of photographs of the skeleton of an old male Kivu Gorilla (*Gorilla gorilla beringeri* Matschie), the property of Lord Rothschild, and also a series of photographs showing the milk-dentition in the skull of a young African Elephant.

On behalf of Lord Rothschild, Mr. Gerrard exhibited the mounted specimen of the Kivu Gorilla (mounted by Messrs. Rowland Ward), and stated that it differed from the other races of Gorilla externally by its long thick pelage, intense black colouring, and large fleshy protuberance on the top of the head.

Mr. D. Seth-Smith, F.Z.S., exhibited a series of skins and photographs of some polyandrous Birds, and described their mating habits.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Dr. CHAS. F. SONNTAG, F.Z.S., exhibited, and made remarks upon, some abnormalities in the Carnivora.

Mr. L. T. HOGBEN, F.Z.S., and Mr. E. A. SPAUL, exhibited, and made remarks upon, the effect of Pineal Gland administration on the pigment-cells of Frog Tadpoles.

Mr. R. I. POCOCK, F.R.S., F.Z.S., communicated his paper on "The Auditory Bulla and other Cranial Characters in the Mustelidæ (Martens, Badgers, etc.)."

In the absence of the Author, Mr. G. S. THAPAR's paper "On the Venous System of the Lizard, *Varanus bengalensis* Daud.," was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, May 24th, at **5.30** P.M., when the following communications will be made:—

The SECRETARY.

Report on the Additions to the Society's Menagerie during the month of April, 1921.

CHAS. F. SONNTAG, M.D., F.Z.S., Anatomist to the Society.

The Comparative Anatomy of the Tongues of the Mammalia.—IV. Families 3 and 4. Cebidæ and Hapalidæ.

R. BROOM, F.R.S., C.M.Z.S.

On some new Genera and Species of Anomodont Reptiles from the Karroo Beds of South Africa.

R. I. POCOCK, F.R.S., F.Z.S.

On the External Characters of some Species of *Lutrinæ* (Otters).

C. W. ANDREWS, D.Sc., F.R.S., F.Z.S.

Note on the Skull of *Dinotherium giganteum* in the British Museum.

The following Papers have been received:—

Dr. C. F. Sonntag, F.Z.S.

The Comparative Anatomy of the Koala (*Phascolarctos cinereus*) and the Vulpine Phalanger (*Trichosurus vulpecula*).

R. I. Pocock, F.R.S., F.Z.S.

The External Characters of the Koala (*Phascolarctos*) and some related Marsupials.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

Zoological Society of London,
Regent's Park, London, N.W. 8.
May 17th, 1921.

No. 218.

ABSTRACT OF THE PROCEEDINGS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.*

May 24th, 1921.

Prof. E. W. MacBride, D.Sc., LL.D., F.R.S., Vice-President,
in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the month of April, 1921.

Miss L. E. Cheesman, F.E.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the habits in the larval stage of the Hydropsychidæ (Snare-building Caddis Worms).

Major Stanley S. Flower, F.Z.S., exhibited examples of three species of Egyptian Jerboas—*Jaculus jaculus*, *Jaculus orientalis*, and *Scarturus tetradactylus*, the latter being the first living specimens ever brought to England; and made remarks upon the distribution of the three species in North Africa.

Dr. C. W. Andrews, F.R.S., F.Z.S., gave a *résumé* of his paper "On the Skull of *Dinotherium giganteum* in the British Museum."

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Dr. Chas. F. Sonntag, F.Z.S., gave a *résumé* of his papers (1) "The Comparative Anatomy of the Tongues of the Mammalia, Families 3 and 4, Cebidæ and Hapalidæ," and (2) "Some Points in the Anatomy of the Tongues of the Lemuroidea."

In the absence of the Author, Prof. R. Broom, F.R.S., C.M.Z.S., his paper, "On some new Genera and Species of Anomodont Reptiles from the Karroo Beds of South Africa," was taken as read.

Mr. R. I. Pocock, F.R.S., F.Z.S., gave a *résumé* of his paper "On the External Characters of some Species of *Lutrinæ* (Otters)."

The next Meeting of the Society for Scientific Business will be held on Tuesday, June 7th, at **5.30** p.m., when the following communications will be made :—

Dr. Frank M. Chapman.

The Distribution of Bird-life in the Urubamba Valley of Peru. (Illustrated by lantern-slides.)

S. Maulik, F.Z.S.

New Indian Drilid Beetles.

Prof. J. P. Hill, F.R.S., V.P.Z.S.

Exhibition of some Marsupial Embryos, especially the Koala and the Wombat.

R. I. Pocock, F.R.S., F.Z.S.

The External Characters of the Koala (*Phascolarctos*) and some related Marsupials.

Dr. C. F. Sonntag, F.Z.S.

The Comparative Anatomy of the Koala (*Phascolarctos cinereus*) and the Vulpine Phalanger (*Trichosurus vulpecula*).

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
May 31*st*, 1921.

No. 219.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

June 7th, 1921

Prof. J. P. Hill, F.R.S., Vice-President,
in the Chair.

Major Stanley S. Flower, O.B.E., F.Z.S., exhibited, and made remarks upon, some living specimens of *Testudo leithii* and an example of *Testudo ibera*.

Dr. P. Chalmers Mitchell, C.B.E., F.R.S., exhibited, and made remarks upon, a photograph of the Death-mask of a young Gorilla, presented to the Society by Prof. Howard Macgregor, of Columbia University, New York.

Dr. Frank M. Chapman gave an account of the distribution of Bird-life in the Urubamba Valley of Peru, and illustrated his remarks with a remarkable series of lantern-slides.

In the absence of the Author, Mr. S. Maulik's paper on "New Indian Drilid Beetles" was taken as read.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Prof. J. P. HILL, F.R.S., V.P.Z.S., exhibited, and made remarks upon, a series of lantern-slides of some Marsupial Embryos, dealing especially with the Koala (*Phascolarctos*) and the Wombat (*Phascolomys*).

Mr. R. I. POCOCK, F.R.S., F.Z.S., gave a *résumé* of his paper on "The External Characters of the Koala (*Phascolarctos*) and some related Marsupials."

Owing to the lateness of the hour, Dr. C. F. SONNTAG's paper on "The Comparative Anatomy of the Koala (*Phascolarctos*) and the Vulpine Phalanger (*Trichosurus vulpecula*)" and Mr. C. TATE REGAN's paper on "The Cichlid Fishes of Lake Nyassa" were taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, October 18th, 1921, at **5.30** P.M.

A notice stating the Agenda for the Meeting will be circulated early in October.

The following Paper has been received:—

R. I. POCOCK, F.R.S., F.Z.S.

The External Characters and Classification of the Mustelidæ.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
June 14th, 1921.

No. 220.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

October 18th, 1921.

Sir S. F. Harmer, K.B.E., Sc.D., F.R.S., Vice-President, in the Chair.

The Secretary read a Report upon the Additions to the Society's Menagerie during the months of June, July, August, and September, 1921.

Mr. M. A. C. Hinton exhibited, and made remarks upon, an embryo African Elephant.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon, photographs of a Common Grass-Snake swallowing a Viper.

Mr. F. Martin Duncan, F.Z.S., exhibited a series of cinematograph films of Marine Animals, and asked the Society to accept the series for its Zoological Film Library.

Mr. D. Seth-Smith, F.Z.S., exhibited a series of photographs of the Sacred Ibis nesting in the Society's Gardens, and said that the last occasion on which the birds had bred in the Gardens was in 1877, as recorded by the late Dr. P. L. Sclater in 'The Ibis' (1878, ser. 4, vol. ii. p. 449).

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Prof. G. Elliot Smith, F.R.S., F.Z.S., gave an account of the habits of *Tarsius*, and illustrated his remarks by a series of photographs of living specimens which had been taken by Mr. W. E. Le Gros Clark, F.Z.S., in Borneo.

In the absence of Mr. Stanley Hirst, F.Z.S., a *résumé* of his paper "On some new Parasitic Mites," was given by Prof. S. Maulik, F.Z.S.

In the absence of the Author, Prof. J. Playfair McMurrich's paper "Note on the Systematic Position and Distribution of the Actinian, *Sagartia luciæ*," was taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 8th, at **5.30** p.m., when the following communications will be made:—

Edgar P. Chance, M.A., M.B.O.U.

The Laying-habits of the Cuckoo (*Cuculus canorus*) and the Life of the young Cuckoo.

W. Rae Sherriffs, M.A., D.Sc.

Evolution within the Genus.—Part I. *Dendronephthya* (*Spongodes*), with Descriptions of a Number of Species. Part II. Description of Species (Alcyonaria) taken by the 'Siboga' Expedition.

Dr. Chas. F. Sonntag, F.Z.S.

The Comparative Anatomy of the Tongues of the Mammalia.—V. Lemuroidea and Tarsioidea. VI. Summary and Classification of the Tongues of the Primates.

R. I. Pocock, F.R.S., F.Z.S.

The External Characters and Classification of the Mustelidæ.

The following Papers have been received :—

CHAS. F. SONNTAG, M.D., F.Z.S.

Contributions to the Visceral Anatomy and Myology of the Marsupialia.

C. W. HOBLEY, C.M.G., C.M.Z.S.

The Fauna of East Africa and its Future.

H. MATSUMOTO.

Megalohyrax Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt.

The Publication Committee desire to remind Fellows that it is only by courtesy that they are allowed to bring guests to a Scientific Meeting. For the present no Fellow can be permitted to bring more than one guest to a Meeting.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
October 25th, 1921.

No. 221.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 8th, 1921.

Dr. A. Smith Woodward, F.R.S., Vice-President,
in the Chair.

Mr. R. I. Pocock, F.R.S., F.Z.S., gave a *résumé* of his paper on "The External Characters and Classification of the Mustelidæ."

In the absence of the Author, Dr. W. Rae Sherriff's paper "Evolution within the Genus.—Part I. *Dendronephthya* (*Spongodes*), with Descriptions of a Number of Species. Part II. Description of Species (Alcyonaria) taken by the 'Siboga' Expedition," was taken as read.

Dr. Chas. F. Sonntag, F.Z.S., gave a *résumé* of his paper "The Comparative Anatomy of the Tongues of the Mammalia.—V. Lemuroidea and Tarsoidea. VI. Summary and Classification of the Tongues of the Primates."

Mr. Edgar P. Chance, M.A., M.B.O.U., gave an account of his investigation of the Laying-habits of the Cuckoo (*Cuculus*

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

canorus) and the Life of the young Cuckoo, and illustrated his remarks with a striking series of cinematograph films and photographs.

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 22nd, at **5.30** P.M., when the following communications will be made:—

Dr. A. Smith Woodward, V.P.Z.S., F.R.S.

Exhibition of a Fossil Human Skull from Broken Hill, North Rhodesia.

Chas. F. Sonntag, M.D., F.Z.S.

Contributions to the Visceral Anatomy and Myology of the Marsupialia.

C. W. Hobley, C.M.G., C.M.Z.S.

The Fauna of East Africa and its Future.

H. Matsumoto.

Megalohyrax Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt.

The following Paper has been received:—

J. Stephenson, D.Sc., F.Z.S.

Contributions to the Morphology, Classification, and Zoogeography of Indian Oligochaeta:—

IV. On the diffuse Production of Sexual Cells in a Species of *Chætogaster* (Fam. Naididæ).

V. On *Drawida japonica* (Michlsn.), a Contribution to the Anatomy of the Moniligastridæ.

VI. On the Relationships of the Genera of Moniligastridæ; with some Considerations on the Origin of Terrestrial Oligochæta.

The Publication Committee desire to remind Fellows that it is only by courtesy that they are allowed to bring guests to a Scientific Meeting. For the present no Fellow can be permitted to bring more than one guest to a Meeting.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited as far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 15th, 1921.

No. 222.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 22nd, 1921.

Prof. E. W. MacBride, F.R.S., Vice-President, in the Chair.

Mr. A. S. Le Souëf, C.M.Z.S., exhibited, and made remarks upon, a series of lantern-slides illustrating the early life-history of *Ornithorhynchus*.

Dr. A. Smith Woodward, F.R.S., V.P.Z.S., exhibited, and made remarks upon, a Human Skull and other remains from Broken Hill, North Rhodesia, upon which he had founded the species *Homo rhodesiensis*. In comparing the Rhodesian skull with a Neanderthal skull from La Chapelle, Dr. Smith Woodward stated that the former may prove to be the next grade after Neanderthal in the ascending series.

With the consent of the Author, the communication of Mr. C. W. Hobley's paper on "The Fauna of East Africa and its Future," was postponed.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Dr. Chas. F. Sonntag's paper "Contributions to the Visceral Anatomy and Myology of the Marsupialia," and Prof. H. Matsumoto's paper on "*Megalohyrax* Andrews and *Titanohyrax*, g. n.—A Revision of the Genera of Hyracoids from the Fayûm, Egypt," were taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 7th, 1922, at **5.30** P.M.

A notice stating the Agenda for that Meeting will be circulated in January.

The following Papers have been received:—

J. Stephenson, D.Sc., F.Z.S.

Contribution to the Morphology, Classification, and Zoogeography of Indian Oligochæta:—

IV. On the diffuse Production of Sexual Cells in a Species of *Chætogaster* (Fam. Naididæ).

V. On *Drawida japonica* (Michlsn.), a Contribution to the Anatomy of the Moniligastridæ.

VI. On the Relationships of the Genera of Moniligastridæ; with some Considerations on the Origin of Terrestrial Oligochæta.

R. Broom, D.Sc., F.R.S., C.M.Z.S.

On the Temporal Arches of the Reptilia.

The Publication Committee desire to remind Fellows that it is only by courtesy that they are allowed to bring guests to a Scientific Meeting. For the present no Fellow can be permitted to bring more than one guest to a Meeting.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

Zoological Society of London,
Regent's Park, London, N.W. 8.
November 29th, 1921.

Indian Agricultural Research Institute (Pusa)
LIBRARY, NEW DELHI-110012

This book can be issued on or before....................

Return Date	Return Date